MODELLING AND ANALYSIS OF POPULATION MODELS IN HOMOGENEOUS AND TWO-PATCH HABITATS: EFFECT OF SUPPLEMENTARY RESOURCE

A Thesis Submitted

in Partial Fulfilment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

by

JOYDIP DHAR

to the

DEPARTMENT OF MATHEMATICS

INDIAN INSTITUTE OF TECHNOLOGY KANPUR

August, 1997

Certificate

It is certified that the work contained in the thesis entitled "*Modelling and Analysis of Populatio[n] Models in Homogeneous and Two-Patch Habitats: Effect of Supplementary Resource*", by Mr **Joydip Dhar**, has been carried out under my supervision and that this work has not bee[n] submitted elsewhere for a degree.

August, 1997

Jang B Shu[kla]

Dr. J. B. Shukla
Professor
Department of Mathematic[s]
I.I.T. Kanpur

To
My Mother and Father
With
Profound Respect

Synopsis

In modern times, due to various environmental factors such as industrialization, pollution, deforestation, etc., the animal habitats are affected all around the world. The deforestation caused by industrial and human activities has a very detrimental effect on biological populations in a forest habitats leading to loss of biodiversity, the important reasons being depletion of resource, patchiness of habitats and population migration (diffusion). One example, where forest habitat has been destroyed by industrialization, causing patchiness, is the Doon Valley in Utter Pradesh, India, where ecological stability is threatened. Therefore, the study of population dynamics with diffusion and explicit dependence of populations on resources in both homogeneous and patchy habitats is an important area of research in the field of mathematical ecology dealing with survival of species.

It may be noted here that the study releted to the dynamics of two or more interacting populations in a patchy habitat with diffusion and resource dependence is very limited. Also, the effect of supplementary resource on population dynamics in patchy habitats is a new area of research in mathematical ecology. In view of the above, in this thesis, the effect of patchiness as well as of supplementary resource on a single species, prey-predator and competing species systems are investigated by using qualitative theory of differential equations.

The work embodied in this thesis is divided into seven chapters. Chapter 1, is concerned with general introduction and literature survey relevant to population dynamics with diffusion in homogeneous and patchy habitats. The literature related to alternative or supplementary resource on interacting populations has also been reviewed briefly in this chapter.

In chapter 2, a general single species harvesting model with diffusion in a linear two-patch habitat, under both the reservoir and no-flux boundary conditions and a continuous flux matching condition at the interface, is studied. It is shown that there exists a unique positive, continuous, monotonic steady state solution under both setsof boundary conditions. The linear and nonlinear stability behavoir of the non-uniform and uniform steady state cases, have been discussed and the corresponding conditions are determind.

In chapter 3, a general single species model with diffusion in a linear two-patch habitat, under both the reservoir and no-flux boundary conditions and a continuous flux matching condition at the interface, is investigated again by considering the dependence of the population on a supplementary resource. It is shown that the behavoir of the steady state solution is same as in chapter 2, but the level of steady state distribution of the species population is higher at each location in the habitat due to the presence of the supplementary self-renewable resource.

In chapter 4, a prey-predator type model with diffusion in a homogeneous and two-patch habitats, under both the reservoir and no-flux boundary conditions and a continuous flux matching condition at the interface, is studied. It is shown that the steady state solutions of both the species are positive, continuous and monotonic in the two-patch habitat. By comparing the results with the homogeneous habitat, it has been observed that the diffusion may increase the stability, but the patchiness destabilizes the system.

In chapter 5, the same prey-predator system as in chapter 4, but with a supplementary self-renewable resource for the prey population in a two-patch habitat, is investigated. The behavoir of the steady state solutions have been shown to be the same as in chapter 4, but the level of steady state distributions of prey and predator population are correspondingly greater, in the presence of the supplementary resource for the prey.

In chapter 6, a two species competition model with diffusion in a homogeneous and two-patch habitats, under both the reservoir and no-flux boundary conditions and a continuous flux matching condition at the interface, is studied. It is found that in this case also, similar as in chapter 4, the steady state solutions of both the species are positive, continuous and monotonic in the two-patch habitat. Further, by comparing the results with the homogeneous case, it is noted that in this case also the diffusion may increase the stability, but the patchiness destabilizes the system.

In chapter 7, the same competing system as in chapter 6, with a common supplementary resource for both the species in two-patch habitat, is modelled and analyzed. The behavoir of the steady state solutions of both the species are same as in chapter 6, but the level of steady state distributions of both the populations are correspondingly greater, in the presence of a common self-renewable supplementary resource.

ACKNOWLEDGEMENT

I express my heartfelt gratitude to my thesis supervisor, Professor J. B. Shukla, for his interest, constructive criticism, excellent rapport, indefatigable encouragement throughout the research program. I extend my thanks and profound respect to Professor H. I. Freedman, Applied Mathematics Institute, University of Alberta, Edmonton, Canada, for valuable suggestion and constructive criticism.

I acknowledge with pleasure the cooperation and help received from all faculty members, Department of Mathematics, I.I.T. Kanpur.

I would like to thank all my friends and well wishers especially Dipak, Pramananda, Alok, Arvind, Bhuvanesh, G.K., Pandayji, Johuri, Gautam, Paritosh, Swapan, B.P., Jal, Bishu, Indra, Shusmita, Mini and many others for their enthusiastic help throughout my stay at I.I.T. Kanpur making it a memorable and pleasant one.

I take this opportunity to express my respect and thankfulness to my well wishers and colleagues Prof. J.K. Sharma, Prof. S.N. Saha, Dr. Sanjay Srivastava, Dr. Gagan Gupta, Mr. H.S. Payel, Mr. Narayan Misra, Mr. Surinder Singh and many others at Beant College of Engineering and Technology, Gurdaspur.

Above all, I fell very much obliged to my parents and all others family members for what I have received from them by way of inspiration, love, encouragement and moral support.

August, 1997

JOYDIP DHAR

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Chapter 1

General Introduction

1.1 Introduction

In modern times, due to various factors such as industrialization, pollution, deforestation etc., the animal habitats are affected all around the world. The deforestation caused by industrial and human activities has detrimental effects on biological populations in a forest habitat leading to extinction of certain rare species affecting biodiversity, the important reasons being depletion of resources, patchiness of the habitat and population migration (diffusion). One example, where forest habitat has been destroyed by industrialization, causing patchiness and resource depletion, is the Doon Valley in Utter Pradesh, India [118], where ecological stability is threatened. Therefore, the study of population dynamics in both homogeneous and patchy habitats with diffusion and explicit dependence of population on resource is an important area of research in the field of mathematical biology dealing with survival of species.

The evolution and existence of species has been the subject of scientific investigation since the days of Darwin and studies were mainly in the form of experimental observations. The first major mathematical attempt in this direction was due to Lotka (1924), and Volterra (1926), which is the main theme of deterministic theory of population dynamics in

mathematical biology. Over the last seventy years, many models for two or more interacting species have been proposed on the basis of Lotka and Volterra models by taking into account the effects of crowding, age structure, time delay, functional response, harvesting, toxicants, habitat changes, etc. [Rescigno [105], May [85], Cushing [22, 23], Harada and Fukao [53], Gopalsamy [42, 43, 44], Hsu and co-authors [61, 62, 66, 67], Freedman [28, 29, 31], Cheng et al. [15], Freedman and Gopalsamy [33, 34], Yodzis [137], Hallam [49, 50, 51, 52], Kapur [74], Hutson and Viskers [70], Takeuchi [126, 127], Mitra et al. [91], Bonan [9], Shukla et al. [115, 118, 119, 120, 121], Shukla and Dubey [114, 116, 117] etc.].

However, in the original Lotka-Volterra model, spatial variation has not been considered. It may be noted that Lotka-Volterra model focuses on population interactions at a point in the space ignoring movement (migration) which means a perfect mixing of the species in a given region. Mathematically, this is equivalent to assuming that the dispersal rates are sufficiently high, and the population in the habitat are well mixed. It is nevertheless true that time and space are inseparable "sister coordinates", and only when population dynamics of organisms are studied in both time and space can the ecological situation be understood in it's reality [Levin [82, 83, 84], Okubo [100]].

1.2 Migration of Population

As mentioned above, due to environmental factors and other related effects, the tendency of the species living in the habitat is to migrate to better suited regions for their survival and existence. In general the movement of the species in the habitat may arise due to certain factors such as overcrowding, anticlimate, predator chasing prey, refuge, and fugitive strategies and more importantly due to resource (food) limitation (i.e. availability) in the habitat, Verma [131].

Experimental investigation of the phenomenon of animal dispersion was first conducted, for insects. Dobzhansky and Wright [24, 25] have done the famous experiments on

the release of Drosophila flies, and later Dobzhansky and Powell studied the rates of dispersal of Drosophila pseudoobscura in the habitat. Some Japanese entomologists [Watanabe et al. [133], Kono [77], Ito [71] and Morisita [92, 93]], also contributed to the concept of biological diffusion by including interactive forces between dispersing individuals in the form of "density-dependent dispersion". They emphasized that a model of dispersion must consider the forces operating between population individuals, and it cannot be limited to the simple random walk. Several other experimental studies have also been conducted on dispersion of Predator-Prey systems [Okubo [100], Huffaker [68, 69], Bergerud et al. [6], Bergerud and Page [7]].

A typical species may have dispersive migration in a particular direction due to favorable environmental and ecological conditions in that direction but it may have no migration in other direction. The first successful attempt to study the migration of the species mathematically is due to the Skellam [122] using the concept of random dispersal. Since then, several investigators [Rosen [106, 107], Rothe [108, 109, 110], Fife [27], Shigesada [112], Okubo [100], Shigesada and Roughgarden [113], Allen [1, 2, 3], Cantrell and Cosner [11, 12], Pao [102, 103, 104]], studied the effects of migration on local and global stability of interacting species system by considering Lotka-Volterra and other types of prey predator and competition models [see also Levin [82, 83, 84] and Verma [131]].

The effects of diffusion on population dynamics, since individuals interact and move about in the habitat, can be described by the continuous space-time interaction-migration models. The principal ingredients of these models are equations of the form

$$\frac{\partial u}{\partial t} = \mathbf{F}(u) + D\Delta u \tag{1.1}$$

where u is an n-vector (each component represents the density of one species), D is a matrix (diffusion coefficients matrix), and Δ is the Laplace operator in the spatial coordinates. The vector $\mathbf{F}$ is a catch-all term describing all reactions and interactions. Using (1.1) various population models with diffusion for single species and interacting populations in both homogeneous and heterogeneous environment, have been proposed and analyzed, [see the

review article by Levin [83, 84] and McMurtrie [86]]. Several good examples of this type can be found in the monographs by Fife [27] and Okubo [100], which also provide a overview of the study of self-organizing phenomena in biology.

Some workers have also studied the coexistence, persistence and extinction in single species and the Lotka-Volterra reaction diffusion models [Gopalsamy [42], Allen [1, 2, 3], Mimmura et al. [88]] and the global stability in generalized Lotka-Volterra with diffusion, Takeuchi [126].

Hadeler and Rothe [48] have studied the effects of dispersion on linear stability of interacting species in the one dimensional homogeneous finite habitat for prey predator system where the dispersion coefficients are equal and constant for both the species. It has been shown that the effect of such dispersion is to stabilize the equilibrium state under nonhomogeneous boundary conditions. Similar analysis has also been carried out by Gopalsamy [42] for competing species in case of homogeneous finite and semi-finite habitats. It is evident from his work that dispersive migration has no effect on the otherwise unstable equilibrium state in the case of semi-infinite habitat while migration may stabilizes the equilibrium state in the case of finite habitat. For unequal but constant dispersion coefficients of the two species, it has been shown that for competition model diffusion may increase the stability of equilibrium state (at least non decreasing), but in the case of prey-predator model diffusion instability occurs, Mimura and Nishida [89], and Jorne [73].

In general, a diffusion process in an ecosystem tends to give rise to a uniform density of population in the habitat. As a consequence, it may be expected that diffusion, when it occurs, plays the general role of increasing stability in a system of mixed populations and resources. However there is an important exception, known as "diffusion induced instability" or "diffusive instability". This exception might not be a rare event especially in prey-predator systems [129, 136].

Levin [83] has given two examples of prey-predator model where he studied the role of diffusion by suitably choosing function $\mathbf{F}(u)$ in equation (1.1).

Model 1: Lotka-Volterra Model (S_1:prey, S_2:predator)

$$F_1 = \alpha_1 S_1 - \beta_1 S_1 S_2 \text{ and } F_2 = -\alpha_2 S_2 + \beta_2 S_1 S_2, \tag{1.2}$$

where α_1, β_1, α_2, β_2 are positive constants. In this model no diffusive instability occurs.

Model 2: Phytoplankton-Herbivore System (Levin and Segel, 1976)

$$F_1 = a_1 S_1 + eS_1^2 - b_1 S_1 S_2 \text{ and } F_2 = -cS_2^2 + b_2 S_1 S_2, \tag{1.3}$$

this system is seen to have a diffusive instability if $b_1 b_2 > ce$, $b_2 > e$, and furthermore

$$\frac{D_2}{D_1} > \left\{ \left(\frac{b_1}{c}\right)^{1/2} - \left(\frac{b_1}{c} - \frac{e}{b_2}\right)^{1/2} \right\}^{-2} = \theta_c^2 \tag{1.4}$$

Hastings [56] has derived the sufficient conditions for global stability in n-species Lotka-Volterra model with variable diffusion coefficients in a linear habitat (i.e. $0 \leq x \leq L$) under no-flux boundary conditions. He studied the following model,

$$\frac{\partial N_i}{\partial t} = N_i \left(r_i + \sum_{j=1}^{n} a_{ij} N_j \right) + \sum_{k=1}^{m} \frac{\partial}{\partial x_k} \left(D_i \frac{\partial N_i}{\partial x_k} \right) \quad i = 1, \cdots n \tag{1.5}$$

where the D_i's are measures of dispersal rate and may depend on space variable x and time t or any of the N_i. The following boundary conditions,

$$\frac{\partial N_i}{\partial x} = 0, \quad \text{for } t > 0,\ x = 0,\ x = L, \tag{1.6}$$

associated with equation (1.5), imply that the region is truly closed. Hastings [57], also studied a single species model with large diffusion rates and established a necessary and sufficient condition for stability.

Nallaswamy and Shukla [98], consider a dispersal prey-predator model with functional response.

$$\frac{\partial N_1}{\partial t} = N_1 \left(a_1 - a_{11} N_1 - \frac{a_{12} N_2}{1 + \alpha N_1} \right) + \frac{\partial}{\partial x} \left(D_1 \frac{\partial N_1}{\partial x} \right) \tag{1.7}$$

$$\frac{\partial N_2}{\partial t} = N_2\left(-a_2 + \frac{a_{21}N_1}{1+\alpha N_1}\right) + \frac{\partial}{\partial x}\left(D_2\frac{\partial N_2}{\partial x}\right) \tag{1.8}$$

It is shown by analyzing this model that the functional response has a destabilizing effect. They have shown that there is no diffusive instability, even with functional response. They further established that if the equilibrium state is linearly stable, a subregion of the positive quadrant can be found in the phase plane where it is nonlinearly stable with or without diffusion. Shukla et al. [119] also studied the effects of dispersal in a multi-species food chain model.

Timm and Okubo [129], considered the Levin-Segel model [84], and extended it to plankton populations with time-varying diffusivities. The local stability of uniform equilibria is examined both analytically and numerically. They found that diffusive instability is less likely to occur in systems with time-varying diffusivity than those with constant diffusivity.

Recently, Pao [102, 103, 104], studied the reaction diffusion equations with nonlocal boundary and initial conditions and, Takeuchi and Lu [128] considered a diffusive competitive Lotka-Volterra model, and studied the permanence and global stability of the system.

1.3 Patchy Habitat

The real habitats are both homogeneous and heterogeneous as regards to their environmental and ecological characteristics. Heterogeneity can arise due to topographical, geographical and other environmental conditions. Seasonal climatic changes can also affect the heterogeneity of the habitat. In general in a habitat, patchiness, a type of heterogeniety, occurs due to discontinuous variations in geographical, ecological and environmental (including climatic changes) characteristics, Verma [131]. As regards to the forest habitats, patchiness can arise due to industrialization, pollution and population.

Thus, in reality, one may visualize a habitat to be patchy if its ecological characteristics are constants but different in each patch. For example, the patchy distributions of plankton in the sea and lakes have been well-documented [Cassie [21], Steele [124]]. The mechanism which maintains this patchiness is still, however, a subject of controversy. A few of the various possibilities that have been proposed are : (1) behavioral reaction to or association with, temperature, salinity, and nutrient distributions, (2) food-chain association in predator-prey relationships, (3) aggregative behavior for breeding and feeding, (4) deforestation of the habitat caused by industrialization, pollution and population growth [100, 118].

Levin [82, 83, 84] studied the effects of patchiness in a heterogeneous habitat by considering the movement of species from one patch to other as proportional to the difference of densities of the respective species in adjoining patches. The effect of population diffusion on coexistence of species has also been studied in patchy habitats by using both continuous diffusion and discrete diffusion models [Allen [1, 2, 3], Freedman [28, 30, 32], Takeuchi [126, 127], Takeuchi and Lu [128]]. In these studies, it may be noted that the diffusion is considered only across the patches but with in the patch no diffusion of populations are considered.

Verma [131] studied the linear and non-linear stability of uniform steady states corresponding to Lotka-Volterra type competitive species and prey-predator systems in a habitat with diffusion in each of the n-adjoining linear patches. She has shown that the uniform state which is otherwise stable in a homogeneous habitat, also stable in a patchy habitat but with restrictive conditions. In the case of a competition model, she has found that if the equilibrium state is unstable without diffusion, then it can still become stable with diffusion but under more restrictive conditions in the case of a patchy habitat. In the case of prey-predator system the stable equilibrium state with diffusion remains stable in the case of patchy habitat also.

Freedman et al. [38] proposed a single species diffusion model in a two-patch environment. It has been shown that there exists a positive, monotonic, continuous non-uniform steady-state solution with continuous flux, under both the reservoir and no-flux boundary conditions, that is linearly asymptotically stable. Freedman and Wu [40], extended the study of single species model with three-patch environment and analyze the existence, piece wise monotonicity and stability of the steady states with only reservoir boundary conditions. In this paper they use an interesting theorem for topology, namely Topological Translation Theorem, which reduces a "three-patch" problem to "two-patch" problem and "two-patch" to "one-patch". In the same year Freedman and Kriszti [35] also studied a class of single species models with diffusion in a habitat with number of patches. It has been shown that under certain conditions, there is a unique, positive, globally asymptotically stable steady state.

It may be noted here that in the above studies, the stability of non-uniform steady state corresponding to systems of two or more populations having general interaction, in a patchy habitat with diffusion has not been studied. In view of these, in this thesis we study the effect of patchiness on the following systems:

- A general logistic type single species system with harvesting and with diffusion in each patch.
- A general prey-predator system (here predator is partially dependent upon a prey population) with diffusion in each patch.
- A general logistic type two competing species system with diffusion in each patch.

1.4 Effect of Supplementary Resource

In the above we have discussed the growth and existence of population with or without diffusion in a habitat which may be homogeneous or patchy. However, in the real world the

explicit dependence of population on resource or nutrient plays an important role in the growth and existence of these populations. Some laboratory experiment were conducted in [99, 59, 134] on micro-organisms using chemostat to study competition between different populations of microorganisms for a growth limiting nutrient or resource. The mathematical analysis of competing species and several non-interacting populations which depend upon growth limiting nutrient in a chemostat with constant input and variable washout rate have been studied by taking into account Michaelis-Menten kinetics, Hsu et al.[60, 65] and Butler et al. [10]. Some other investigations have also been conducted for the two competing population when the populations are wholly dependent on a self-renewable resource without diffusion in a homogeneous habitat [63, 45, 91]. Recently Freedman and Shukla [37] have studied the effect of an alternative resource for predator on a prey-predator system with diffusion in a homogeneous habitat.

It may be noted here that the above investigations been conducted either without diffusion or with diffusion in a homogeneous habitat and the effect of patchiness of the habitat has not been considered. In this thesis, therefore, we investigate the non-uniform steady state distribution and its stability system by considering diffusion and supplementary resource in two-patch habitat in the following cases:

- A general single species model with a self-renewable supplementary resource.
- A general prey-predator type model with a self-renewable supplementary resource for the prey population.
- A general two species competition type model with a common self-renewable supplementary resource for both the species.

1.5 Summary

This thesis consists of seven chapters and the organization of the thesis is as follows. Chapter-1 deals with general introduction and literature survey relevant to population dynamics with diffusion in homogeneous and patchy habitats. In chapter-2, 4 and 6, the effect of diffusion in both homogeneous and two patch habitats have been studied for single species with harvesting, prey-predator system and the two species competition model using generalized growth rates and interacting functions. In chapter-3, 5 and 7, the role of supplementary resource in a patchy habitat have been modelled and analyzed in the three respective cases of chapter-2, 4, 6.

Bibliography

[1] **Allen, L.J.S.**, Persistence and extinction in Lotka-Volterra reaction-diffusion equations, Math. Biosci., Vol. 65, 1-12, (1983).

[2] **Allen, L.J.S.**, Persistence and extinction in single-species reaction-diffusion populations, Bull. Math. Biol., Vol. 45(2), 209-227, (1983).

[3] **Allen, L.J.S.**, Persistence, extinction and critical patch number for island populations, J. Math. Biol., Vol. 24, 617-625, (1987).

[4] **Anderson, N.** and **Arthurs, A.M.**, Analytical boundary functions for diffusion problems with Michaelis-Menten kinetics, Bull. Math. Biol., Vol. 47(1), 145-153, (1985).

[5] **Angulo, J.** and **Linares, F.**, Global existence of solutions of a nonlinear dispersive model, J. Math. Anal. & Appl., Vol. 195(3), 797-808, (1995).

[6] **Bergerud, A.T.**, **Butler, H.E.** and **Miller, D.R.**, Antipredator tactics of calving caribou: dispersion in mountains, Can. J. Zool., Vol. 62, 1566-1575, (1984).

[7] **Bergerud, A.T.** and **Page, R.E.**, Displacement and dispersion of parturient caribou at calving as antipredator tactics, Can. J. Zool., Vol. 65, 1597-1606, (1987).

[8] **Bergman, E.** and **Greenberg, L.A.**, Competition between a planktivore, a benthivore and a species with ontogenetic diet shifts, Ecology, Vol. 75(5), 1233-1245, (1994).

[9] **Bonan, G.B.**, Analysis of neighborhood competition among annual plants: Implication of a plant growth model, Ecological Modelling, Vol. 65, 123-136, (1993).

[10] **Butler, G.J.** and **Wolkowicz**, A mathematical model of the chemostat with a general class of functions describing nutrient uptake, SIAM J. Appl. Math., Vol. 45(1), (1985).

[11] **Cantrell, R.S.** and **Cosner, C.**, On the steady-state problem for the Volterra-Lotka competition model with diffusion, Houston J. Math., Vol. 13, 337-352, (1987).

[12] **Cantrell, R.S.** and **Cosner, C.**, Diffusive logistic equations with indefinite weights: population models in disrupted environments, Proc. of the Royal Society of Edinburgh, Vol. 112A, 293-318, (1989).

[13] **Capasso, V.**, Global solution for a diffusive nonlinear deterministic epidemic model, SIAM J. Appl. Math., Vol. 35, 274-284, (1978).

[14] **Casten, R.G.** and **Holland, C.J.**, Instability results for reaction diffusion equations with Neumann boundary conditions, J. Differ. Equations, Vol. 27, 266-273, (1978).

[15] **Cheng, K.S.**, **Hsu, S.B.** and **Lin, S.S.**, Some results on global stability of a predator-prey systems, J. Math. Biol., Vol. 12, 115-126, (1981).

[16] **Chow, P.L.** and **Tam, W.C.**, Periodic and traveling wave solutions to Volterra-Lotka equations with diffusion, Bull. Math. Biol., Vol. 38, 643-658, (1976).

[17] **Cohen, D.S.** and **Murray, J.D.**, A generalized diffusion model for growth and dispersal in a population, J. Math. Biol., Vol. 12, 237-249 (1981).

[18] **Comins, H.N.** and **Blatt, D.W.E.**, Prey predator models in spatially heterogeneous environment, J. Theor. Biol., Vol. 48, 75-83 (1974).

[19] **Conway, E.**, **Hoff, D.** and **Smoller, J.**, Large time behavior of solutions of systems of nonlinear reaction-diffusion equations, SIAM J. Appl. Math., Vol. 35(1), 1-16, (1978).

[20] **Conway, E.** and **Smoller, J.**, A comparison theorem for systems of reaction-diffusion equations, Comm. Partial Differential Equations, Vol. 2, 679-697, (1977).

[21] **Cosner, C.** and **Laser, A.C.**, Stable coexistence states in the Volterra-Lotka competition model with diffusion, SIAM J. Appl. Math., Vol. 44, 1112-1132, (1984).

[22] **Cushing, J.M.**, Time delays in single species growth models, J. Math. Biol., Vol. 4, 257-264, (1977).

[23] **Cushing, J.M.**, Two species competition in a periodic environment, J. Math. Biol., Vol. 10, 385-400, (1980).

[24] **Dobzhansky, T.** and **Wright, S.**, Genetics of natural populations. X. Dispersion rates in Drosophila pseudoobscura, Genetics, Vol. 28, 304-340, (1943).

[25] **Dobzhansky, T.** and **Wright, S.**, Genetics of natural populations. XV. Rate of diffusion of a mutant gene through a population of Drosophila pseudoobscura, Genetics, Vol. 32, 303-324, (1947).

[26] **Edelstein-Keshet, L.**, Mathematical Models in Biology, New York, Random House, (1988).

[27] **Fife, P**, Mathematical aspects of reacting and diffusing systems, Lecture Notes in Biomathematics, Vol. 28, Berlin, Springer-Verlag, (1979).

[28] **Freedman, H.I.**, Graphical stability, enrichment and pest control by a natural enemy, Math. Biosci., Vol. 31, 207-225, (1976).

[29] **Freedman, H.I.**, Stability analysis of a predator-prey system with mutual interference and density-dependent death rates, Bull. Math. Biol., Vol. 41, 67-78, (1979).

[30] **Freedman, H.I.**, Single species migration in two habitats: Persistence and extinction, Math. Modelling, Vol. 8, 778-780, (1987).

[31] **Freedman, H.I.**, Deterministic Mathematical Models in Population Ecology, HIFR Consulting Ltd, Edmonton (1987).

[32] **Freedman, H.I.**, Persistence and extinction in models of two-habitat migration, Math. Comput. Modelling, Vol. 12(1), 105-112, (1989).

[33] **Freedman, H.I.** and **Gopalsamy, K.**, Global stability in time-delayed single-species dynamics, Bull. Math. Biol., Vol. 48(5/6), 485-492, (1986).

[34] **Freedman, H.I.** and **Gopalsamy, K.**, Nonoccurence of stability switching in systems with discrete delays, Cand. Math. Bull., Vol. 31(1), (1988).

[35] **Freedman, H.I** and **Kriszti, T.**, Global stability in model of population dynamics with diffusion, I. Patchy Environment, Proc. Royal Soc. of Edinburgh, Vol. 122A, 69-84, (1992).

[36] **Freedman, H.I., Rai, B.** and **Waltman, P.**, Mathematical models of population interactions with dispersal II: Differential survival in a change of habitat, J. Math. Anal. & Appl., Vol. 115(1), (1986).

[37] **Freedman, H.I.** and **Shukla, J.B.**, The effect of a predator resource on a diffusive predator-prey system, Natural Resources Modeling, Vol. 3(3), 359-383, (1989).

[38] **Freedman, H.I., Shukla, J.B.** and **Takeuchi,Y.**, Population Diffusion in a Two-Patch Environment, Math. Biosci., Vol. 95, 111-123, (1989).

[39] **Freedman, H.I.** and **Waltman, P.**, Mathematical models of population interactions with dispersal I: Stability of two habitats with and without a predator, SIAM J. Appl. Math., Vol. 32(3), 631-648, (1977).

[40] **Freedman, H.I.** and **Wu, J.**, Steady-state analysis in a model for population diffusion in a multi-patch environment, Nonlinear Analysis, Theory, Methods & Applications, Vol. 18(6), 517-542, (1992).

[41] **Friedman, A.**, Partial differential equations of parabolic type, Prentice-Hall, Englewood Cliffs, NJ, (1964).

[42] **Gopalsamy, K.**, Competition, dispersion and co-existence, Math. Bio. Sci., Vol. 33, 25-33, (1977).

[43] **Gopalsamy, K.**, Optimal stabilization and harvesting in logistic population models, Ecol. Modelling, Vol. 11, 67-69, (1980).

[44] **Gopalsamy, K.**, Limit cycles in periodically perturbed population systems, Bull. Math. Biol., Vol. 43(4), 463-485, (1981).

[45] **Gopalsamy, K.**, Convergence in a resource-based competition system, Bull. Math. Biol., Vol. 48(5/6), 681-699, (1986).

[46] **Grundy, R.E.**, Local similarity solutions for the initial-value problem in nonlinear diffusion, IMA J. Appl. Math., Vol. 30, 209-214, (1983).

[47] **Haddock, J.R.**, Liapunov-Razumikhin functions and an invariance principle for functional differential equations, J. Differ. Equations, Vol. 48, 95-122, (1983).

[48] **Hadeler, K.P.** and **Rothe, F.**, Travelling fronts in nonlinear diffusion equations, J. Math. Biol., Vol. 2, 251-263, (1975).

[49] **Hallam, T.G.**, A temporal study of diffusion effects on a population modelled by quadratic growth, Nonl. Anal. Theo. Meth. Appl., Vol. 3, 123 - 133, (1979).

[50] **Hallam, T.G.**, **Clark, C.E.** and **Lassiter, R.R.**, Effects of toxicants on populations: a qualitative approach I. Equilibrium environmental exposure, Ecol. Modelling, Vol. 18, 291-304, (1983).

[51] **Hallam, T.G.**, **Clark, C.E.** and **Jordan, G.S.**, Effects of toxicants on populations: a qualitative approach II. First order kinetics, J. Math. Biol., Vol. 18, 25-37, (1983).

[52] **Hallam, T.G.**, and **De Luna, J.T.**, Effects of toxicants on populations: a qualitative approach III. Environmental and food chain pathways, J. Theor. Biol., Vol. 109, 411-429, (1984).

[53] **Harada, K.** and **Fukao, T.**, Coexistence of competing species over a linear habitat of finite length, Math. Biosci., Vol. 38, 279-291, (1978).

[54] **Hardin, D.P., Takac, P.** and **Webb, G.F.**, Dispersion population models discrete in time and continuous in space, J. Math. Biol., Vol. 28, 1-20, (1990).

[55] **Harrison, G.W.**, Multiple stable equilibria in a predator-prey system, Bull. Math. Biol., Vol. 48(2), 137-148, (1986).

[56] **Hastings, A.**, Global stability in Lotka-Volterra systems with Diffusion, J. Math. Biol., Vol. 6, 163-168 (1978).

[57] **Hastings, A.**, Dynamics of a Single Species in a Spatially Varying Environment: The Stabilizing Role of High Dispersal Rates, J. Math. Biol., Vol. 16, 49-55 (1982).

[58] **Hayes, C.K.**, A new traveling-wave solution of Fisher's equation with density-dependent diffusivity, J. Math. Biol., Vol. 29, 531-537, (1991).

[59] **Herbert, D., Elsworth** and **Telling, R.C.**, The continuous culture of bacteria: a theoretical and experimental study, J. Gen. Microbiol., Vol. 4, 601-622, (1956).

[60] **Hsu, S.B.**, Limiting behavior for competing species, SIAM J. Appl. Math., Vol. 34(4), (1978).

[61] **Hsu, S.B.**, On Global Stability of a Predator-Prey System, Math. Biosci., Vol. 39, 1-10 (1978).

[62] **Hsu, S.B.**, On a resource based ecological competition model with interference, J. Math. Biol., Vol. 12, 45-52, (1981).

[63] **Hsu, S.B.**, On a resource based ecological competition model with interference, J. Math. Biol., Vol. 12, 45-52, (1981).

[64] **Hsu, S.B., Cheng, K.S.** and **Hubbell, S.P.**, Exploitative competition of Microorganisms for two complementary nutrients in continuous cultures, SIAM J. Appl. Math., Vol. 41, 422-444, (1981).

[65] **Hsu, S.B., Hubbell, S.P.** and **Waltman, P.**, A mathematical theory of single-nutrient competitions in continuous cultures of microorganism, SIAM J. Appl. Math., Vol. 32, 366-383 (1977).

[66] **Hsu, S.B.** and **Huang, T.W.**, Global stability for a class of predator-prey systems, SIAM J. Appl. Math., Vol. 55(3), 763-783, (1995).

[67] **Hsu, S.B.** and **Hubbell, S.P.**, Two predators competing for two prey species: An analysis of MacArthur's model, Math. Biosci., Vol. 47, 143-171, (1979).

[68] **Huffaker, C.B**, Experimental studies on predation; dispersion factors and prey predator oscillations, Hilgardia, Vol. 27, 305-329, (1958).

[69] **Huffaker, C.B**, Experimental studies on predation: complex dispersion and levals of food in an Acarinc predator pery interactions, Hilgardia, Vol. 37, 305-309, (1963).

[70] **Hutson, V.** and **Viskers, G.T.**, A criterion for permanent co-existence of species, with an application to a two-prey one predator system, Math. Biosci., Vol. 63, 253-269, (1983).

[71] **Ito, Y.**, The growth from of populations in some aphids, with special reference to the relation between population density and movements, Res. Popul. Ecol. 1, 36-48 (Japanese with English summary), (1952).

[72] **Jensen, A.L.**, Simple models for exploitative and interference competition, Ecol. Modelling, Vol. 35, 113-121, (1987).

[73] **Jorne, J.**, The diffusive Lotka-Volterra oscillating system, J. Theor. Biol., Vol. 65, 133-139, (1977).

[74] **Kapur, J.N.**, The effects of harvesting on competing populations, Math. Biosci., Vol. 51, 175-185, (1980).

[75] **Kerner, E.H.**, Further considerations on statistical mechanics of biological associations, Bull. of Math. Biophys., Vol. 21, 217-255 (1959).

[76] **Kohyama, T.**, Size-structured tree populations in gap-dynamic forest – the forest architecture hypothesis for the stable co-existence of species, J. Ecol., Vol. 81, 131-143, (1993).

[77] **Kono, T.**, Time-dispersion curve: experimental studies on the dispersion of insects (2), Res. Popul. Ecol., Vol. 1, 109-118 (Japanese with English summary), (1952).

[78] **Kung, C.-M.** and **Baltzis, B.C.**, The growth of pure and simple microbial competitions in a moving distributed medium, Math. Biosci., Vol. 111, 295-313, (1992).

[79] **Langlais, M.**, Large time behavior in a nonlinear age-dependent population dynamics problem with spatial diffusion, J. Math. Biol., Vol. 26, 319-346 (1988).

[80] **Leon, J.A.** and **Tumpson, D.B.**, Competition between two species for two complementary or two substituble resources, J. Theor. Biol., Vol. 50, 185-201, (1975).

[81] **Leung, A.**, Stabilities for equilibria of competing species reaction-diffusion equations with homogeneous Dirichlet condition, Funkcialaj Ekvacioj, Vol. 24, 201-210, (1981).

[82] **Levin, S.A.**, Dispersion and population interactions, Am. Nat., Vol. 108, 207-228 (1974).

[83] **Levin, S.A.**, Spatial patterning and the structure of ecological communities, Lectures on Mathematics in the Life Sciences, Vol. 8, (1976).

[84] **Levin, S.A.**, Population model and community structure in heterogeneous environments, in Mathematical Ecology, T.G.Hallam and S.A.Levin,eds.,Springer,New York, 295 - 321 (1986).

[85] **May, R.M.**, Limit cycles in predator-prey communities, Science, Vol. 77, 900-902, (1972).

[86] **McMurtrie, R.**, Persistence and stability of single species and prey-predator system in spatially heterogeneous environments, Math. Biosc., Vol. 39, 11-51 (1978).

[87] **Mimura, M.** and **Kawasaki, K.**, Spatial segregation in competitive interaction-diffusion equations, J. Math. Biol., Vol. 9, 49-64, (1980).

[88] **Mimura, M.**, **Ei, S.-I.** and **Fang, Q.**, Effect of domain shape on co-existence problems in a competition diffusion system, J. Math. Biol., Vol. 29, 219-237, (1991).

[89] **Mimura, M.** and **Nishida, T.**, On a certain semilinear parabolic

system related to Lotka-Volterra's ecological model, Publ. Research Inst. Math. Sci., Kyoto Univ., Vol. 14, 269-282, (1978).

[90] **Misra, O.P.** and **Saxena, V.P**, Effects of environmental pollution on the growth and existence of biological populations: Modelling and stability analysis, Indian J. pure appl. Math. Vol. 22(10), 805-817, (1991).

[91] **Mitra, D.**, **Mukherjee, D.**, **Roy, A.B.** and **Ray, S.**, Permanent coexistence in a resource-based competition system, Ecol. Modelling, Vol. 60, 77-85, (1992).

[92] **Morisita, M.**, Habitat preference and evaluation of environment of an animal: experimental studies on the population density of an ant-lion, *Glenuroides japonicus M'L. (1)*, Physiol. and Ecol., Vol. 5, 1-16, (Japanese with English summary), (1952).

[93] **Morisita, M.**, Measuring of habitat value by the "environmental density" method. In: Statistical Ecology, Patil, G.P., Pielou, E.C., Waters, W.E., (eds.), Vol. 1, 379-401, University Park, Pennsylvania: Penn. State Univ., (1971).

[94] **Murray, J.D.**, Non-existence of wave solutions for the class of reaction-diffusion equations given by the Volterra interacting-population equations with diffusion, J. theor. Biol., Vol. 52, 459-469, (1975).

[95] **Murray, J.D.**, Mathematical Biology, (Biomath. Series, Vol. 19), Berlin Heidelberg New York, Springer, (1989).

[96] **Munn, R.E.** and **Fedorov, V.**, The Environmental assessment, IIASA Project Report, Vol. 1, International Institute for Applied Systems Analysis, Laxenburg, Austria.

[97] **Nallaswamy, R.** and **Shukla, J.B.**, Effects of dispersal on the stability of a Prey-Predator system with functional response, Math. Biosc., Vol. 60, 123-132 (1982).

[98] **Nallaswamy, R.** and **Shukla, J.B.**, Effects of Convective and dispersive migration on the linear stability of a two species system with mutualistic interactions and functional response, Bul. Math. Biol., Vol. 44(2), 271-282, (1982).

[99] **Novick, A.** and **Szilard, L.**, Description of the chemostat, Science, Vol. 112, 715-716, (1950).

[100] **Okubo, A.**, Diffusion and Ecological Problem: Mathematical models, Springer-Verlag, Berlin Heidelberg New York, (1980).

[101] **Pacala, S.W.** and **Roughgarden, J.**, Spatial heterogeneity and interspecific competition, Theor. Pop. Biol., Vol. 21, 92-113, (1982).

[102] **Pao, C.V.**, Coexistence and stability of a competition diffusion system in population dynamics, J. Math. Anal. Appl., Vol. 83, 54-76, (1981).

[103] **Pao, C.V.**, Dynamics of reaction diffusion equations with nonlocal boundary conditions, Quart. Appl. Math., Vol. 53, 173-186, (1995).

[104] **Pao, C.V.**, Reaction diffusion equations with nonlocal boundary and nonlocal initial conditions, J. Math. Anal. & Appl., Vol. 195(3), 702-718, (1995).

[105] **Rescigno, A.**, The struggle for life: I. Two species, Bull. Math. Biophysics, Vol. 29, 377-388, (1967).

[106] **Rosen, G.**, Global theorems for species distributions governed by reaction-diffusion equations, J. Chemical Physics, Vol. 61(9), 3676-3679, (1974).

[107] **Rosen, G.**, Solutions to systems of nonlinear reaction-diffusion equations, Bull. Math. Biol., Vol. 37, 277-289, (1975).

[108] **Rothe, F.**, Convergence to the equilibrium state in the Volterra-Lotka diffusion equations, J. Math. Biol., Vol. 3, 319-324, (1976).

[109] **Rothe, F.**, Solutions for systems of nonlinear Elliptic equations with nonlinear boundary conditions, Math. Meth. in the Appl. Sci., Vol. 1, 543-553, (1979).

[110] **Rothe, F.**, Global Solution of Reaction-Diffusion Systems, Lecture Notes in Math., 1072, Springer-Verlag Berlin Heidelberg New York Tokyo (1984).

[111] **Segel, L.A., Jackson, J.L.**, Dissipative structure: An explanation and an ecological example, J. Theor. Biol., Vol. 37, 545-559 (1972).

[112] **Shigesada, N.**, Spatial distribution of dispersing animals, J. Math. Biol., Vol. 9, 85-96, (1980).

[113] **Shigesada, N.** and **Roughgarden, J.**, The role of rapid dispersal in the population dynamics of competition, Theor. Pop. Biol., Vol. 21, 353 - 372 (1982).

[114] **Shukla, J.B.**, and **Dubey, B.**, Effect of changing habitat on species: Application to Keoladeo National Park, India, Ecol. Modelling, Vol. 86, 91-99, (1996).

[115] **Shukla, J.B., Dubey, B.** and **Freedman, H.I.**, Effect of changing habitat on survival of species, Ecol. Modelling, Vol. 87, 205-216, (1996).

[116] **Shukla, J.B.**, and **Dubey, B.**, Simultaneous effect of two toxicants on biosystem: A mathematical modelling, J. Biol. Systems, Vol. 4(1), 109-130, (1996).

[117] **Shukla, J.B.**, and **Dubey, B.**, Modelling the depletion and conservation of forestry resources: Effects of population and pollution, J. Math. Biology, (in press), (1997).

[118] **Shukla, J.B., Freedman, H.I., Pal, V.N., Mishra, O.P., Agarwal, M.** and **Shukla, A.**, Degradation and subsequent regeneration of a resource: A mathematical model, Ecol. Modelling, Vol. 44, 219-229, (1989).

[119] **Shukla, V.P., Shukla, J.B.**, Multispecies food webs with diffusion, J. Math. Biol., Vol. 13, 339-344, (1982).

[120] **Shukla, V.P., Shukla, J.B.** and **Das, P.C.**, Environmental effects on the linear stability of a three species food chain model, Math. Biosci., Vol. 57, 35-58, (1981).

[121] **Shukla, J.B.** and **Verma, S.**,Effect of convective and dispersive interactions on the stability of two species, Bul. Math. Biol., Vol. 43, 593-610, (1981).

[122] **Skellam, J.G.**, Random dispersal in theoretical populations, Biometrika, Vol. 36, 199-218, (1951).

[123] **Smith, O.L.**, The influence of environment gradients on ecosystem stability, Am. Nat., Vol. 116, 1-24, (1980).

[124] **Steele, J.H.**, Patchiness in: The ecology of the sea, [Cushing, D.H., Walsh, J.J. (ed.)], 98-115, Philadelphia: W.B. Saunders Co., (1976).

[125] **Swan, G.W.**, Solution of linear one-dimensional diffusion equations, Bul. Math. Biol., Vol. 38, 1-13, (1976).

[126] **Takeuchi, Y.**, Global stability in generalized Lotka-Volterra diffusion systems, J. Math. Anal. & Appl., Vol. 116, No.1, (1986a).

[127] **Takeuchi, Y.**, Diffusion effect on stability of Lotka-Volterra models, Bull. Math. Biol., Vol. 48(5/6), 585-601, (1986b).

[128] **Takeuchi, Y.** and Lu, Z., Permanence and global stability for competitive Lotka-Volterra diffusion systems, Nonlinear Analysis, Theory, Methods & Applications, Vol. 24(1), 91-104, (1995).

[129] **Timm, U.** and **Okubo, A.**, Diffusion-driven instability in a predator-prey system with time-varying diffusivities, J. Math. Biol., Vol. 30, 307-320, (1992).

[130] **Turing, A.M.**, The chemical basis of morphogenesis, Phil. Trans. Roy. Soc. London, Vol. B237, 37-72, (1952).

[131] **Verma, S.**, Effects of convective and dispersive migration on stability of interactive species system in heterogeneous habitats, *Ph.D. thesis*, Department of Mathematics, Indian Institute of Technology, Kanpur-208016, India, (1980).

[132] **Voller, R.L.**, Solving Volterra-Lotka systems with diffusion by monotone iteration, J. Math. Biol., Vol. 29, 177-187, (1991).

[133] **Watanabe, S.**, **Utida, S.** and **Yosida, T.**, Dispersion of insect and change of distribution type in its process: experimental studies on the dispersion of insects (1), Res. Popul. Ecol., Vol. 1, 94-108, (Japanese with English summary), (1952).

[134] **Williams, F.M.**, Dynamics of microbial populations, Systems Analysis and Simulation in Ecology, B.Patten, ed., Academic Press, New York, Chapter 3, (1971).

[135] **Williams, S.A.** and **Chow, Pao-Liu**, Nonlinear Reaction-Diffusion Models for Interacting Populations, J. Math. Anal. Appl., Vol. 62, 157-169 (1978).

[136] **Wollkind, D.J.**, **Collings, J.B.** and **Barba, M.C.B.**, Diffusive instabilities in a one-dimensional temperature-dependent model system for a mite predator-prey interaction on fruit trees: Dispersal motility and aggregative preytaxis effects, J. Math. Biol., Vol. 29, 339-362, (1991).

[137] **Yodzis, P.**, The effects of harvesting on competitive systems, Bull. Math. Biol., Vol. 38, 97-109, (1976).

Chapter 2

A Single Species Harvesting Model with Diffusion in a Two-Patch Habitat

2.1 Introduction

Biotic populations are usually distributed heterogeneously in their habitat, and the distribution is often patchy, due to patchiness of the habitat which arises from a variety of mechanisms and processes under various conditions including deforestation in the case of a forest habitat. It would, thus, seem natural to study the population dynamics of a single species by including diffusional effects, in a patchy habitat. Many investigators [4, 9, 11, 12, 13, 14, 15, 17, 18, 20] have shown that in a homogeneous habitat, the diffusion, increases the stability in a system, but this may not always be true, if the habitat is patchy [7, 8, 10, 16].

A model of a single species population living in two patch habitats with migration between them across a barrier was proposed by Freedman and Waltman [11]. The model

was extended by [6, 8] to include the case where species (animals) leaving one habitat does not necessarily reach the other habitat, the existence of a positive equilibrium as a function of barrier strengths was examined.

Also Freedman et al.[10] studied a single species diffusion model by assuming that the habitat consists of two patches and has shown that there exists a positive, monotonic, continuous nonuniform steady state solution that is linearly asymptotically stable under both reservoir (or Dirichlet) and no-flux boundary conditions but it is not globally stable because of patchiness.

Keeping the above [6, 10, 11] in view, in this chapter, we consider the dynamics of a diffusing single species population undergoing harvesting in two adjoining patches with a continuous flux matching condition at the interface. The existence of positive, monotonic, continuous nonuniform steady state solution with continuous flux, under both reservoir and no-flux boundary conditions are studied. Also the stability of both linear and non-linear systems are discussed. This model is proposed keeping in view the patchiness caused by many man made projects in the Doon Valley (India) [19]. The model is also applicable to the Burwash caribou herd, which lives on both sides of the Shakwak Trench in the Kluane mountains of the Yukon territories, Canada. The dynamics of this herd has been discussed in [3].

The organization of this chapter is as follows. In next section we describe the general mathematical model for two patches. In section 2.3 we analyzed our model under reservoir and no-flux boundary conditions in subsection 2.3.1 and 2.3.2 respectively, and the uniform steady state case is discussed in subsection 2.3.3. Finally in section 2.4 we have numerically studied the the unsteady and steady state solution of the system with reservoir boundary conditions.

2.2 Mathematical Model

Consider a habitat consisting of two distinct adjoining or patches labeled by the running variable $i = 1, 2$. There are no restrictions on the way the habitat is partitioned into these patches. They may be identical or different in size; they may represent identical regimes of climate and of soil or nutrient factors, or they may represent distinct such environments, or might simply represent a partitioning of a homogeneous environment. The population dynamics of a single species of logistic type is given by the form of a system of parabolic partial differential equations in the two patches as follows:

$$\frac{\partial N_i(s,t)}{\partial t} = N_i(s,t)\mathrm{g}_i(N_i(s,t)) - N_i\mathrm{p}_i(N_i(s,t)) + D_i\frac{\partial^2 N_i(s,t)}{\partial s^2} \tag{2.1}$$

$$i = 1, 2 \qquad\qquad 0 \le s \le L_2$$

Here the growth rate function $\mathrm{g}_i(N_i)$ and the harvesting function $\mathrm{p}_i(N_i)$ are such that

(H.1):

$$\begin{array}{lll} & \mathrm{g}_i(N_i),\ \mathrm{p}_i(N_i) \in C^2[0,\infty), & \\ \mathrm{g}_i(0) > 0, & \text{and } \forall N_i \ge 0, & \mathrm{g}_i'(N_i) \le 0 \\ \mathrm{p}_i(0) = 0, & \text{and } \forall N_i \ge 0, & \mathrm{p}_i'(N_i) \ge 0. \end{array}$$

When the habitat has carrying capacity K_i in the i-th patch respectively, then $\mathrm{g}_i(K_i) = 0$.

Further, we assume that

(H.2): $\exists\ K_i^* > 0$ such that $\mathrm{g}_i(K_i^*) - \mathrm{p}_i(K_i^*) = 0$

It follows that $K_i^* \le K_i$ and the equality only holds when $\mathrm{p}_i(N_i) = 0$.

Since $\forall N_i \ne K_i^*$,

$$\frac{\mathrm{g}_i(N_i) - \mathrm{p}_i(N_i)}{N_i - K_i^*} = \frac{\mathrm{g}_i(N_i) - \mathrm{g}_i(K_i^*)}{N_i - K_i^*} - \frac{\mathrm{p}_i(N_i) - \mathrm{p}_i(K_i^*)}{N_i - K_i^*} = \mathrm{g}_i'(\xi_i) - \mathrm{p}_i'(\xi_i) < 0,$$

where $min\{N_i, K_i^*\} \le \xi_i \le max\{N_i, K_i^*\}$. Hence,

$$(N_i - K_i^*)[\mathrm{g}_i(N_i) - \mathrm{p}_i(N_i)] < 0, \quad \forall N_i \ne K_i^*. \tag{2.2}$$

At the interface $s = L_1$, the continuous flux matching and continuity conditions are written as

$$D_1 \frac{\partial N_1(L_1,t)}{\partial s} = D_2 \frac{\partial N_2(L_1,t)}{\partial s} \text{ and } N_1(L_1,t) = N_2(L_1,t) \tag{2.3}$$

The model is studied under two sets of (namely, reservoir and no-flux) boundary conditions. In the case of reservoir boundary conditions, we take

$$N_1(0,t) = K_1^* \text{ and } N_2(L_2,t) = K_2^* \tag{2.4}$$

In the case of no-flux boundary conditions, we take

$$\frac{\partial N_1(0,t)}{\partial s} = 0 = \frac{\partial N_2(L_2,t)}{\partial s} \tag{2.5}$$

Finally, the model is completed by assuming some positive initial distribution, that is,

$$N_i(s,0) = \chi_i(s) \ > \ 0, \ \ L_{i-1} \le s \le L_i, \ \ i = 1,2, \tag{2.6}$$

such that $N_1(0,0) = K_1^*$, and $N_2(L_2,0) = K_2^*$. An example of $\chi_i(s)$ may be consider as follows:

$$\chi_i(s) = K_1^* + \frac{(K_2^* - K_1^*)}{L_2} s \ .$$

The existence of non-negative, smooth solutions of the above type of system in a homogeneous habitat is shown in [18]. We also note that in the case of no diffusion, the behavior of solutions of our model is well known (see [5], Chapter 1). At each s in the i-th patch, $N_i(s,t) \to K_i^*$ as $t \to \infty$. Clearly, if $K_1^* \neq K_2^*$, then a constant solution of (2.1) in s is impossible and the problem must be analyzed by using the techniques of two point boundary value problems [1, 2].

2.3 Analysis of the Model

2.3.1 Analysis under Reservoir Boundary Conditions

In this section we show the existence of non-uniform steady state solution of our model (2.1), (2.3), (2.4), and (2.6), following Freedman et al. [38]. This steady state solution is given by

$$D_i \frac{d^2 u_i}{ds^2} + u_i \mathrm{g}_i(u_i) - u_i \mathrm{p}_i(u_i) = 0 \quad i = 1, 2 \tag{2.7}$$

The reservoir boundary conditions are given by

$$u_1(0) = K_1^* \text{ and } \; u_2(L_2) = K_2^* \tag{2.8}$$

At the interface $s = L_1$, we have,

$$D_1 \frac{du_1(L_1)}{ds} = D_2 \frac{du_2(L_1)}{ds}, \quad u_1(L_1) = u_2(L_1) \tag{2.9}$$

We use the result of Freedman and Kriszti [7] to show the existence of the positive steady-state solutions in the form of the following theorem.

Theorem 2.3.1 *The steady-state problem (2.7), has a unique positive solution u.* ∎

Since the functions, $\mathrm{G}_i(u_i) = \mathrm{g}_i(u_i) - \mathrm{p}_i(u_i)$ are such that $\mathrm{G}_i(0) > 0$, $\mathrm{G}_i'(u_i) \leq 0$, for $u_i \geq 0$ and $\mathrm{G}_i(K_i^*) = 0$, therefore, $\mathrm{G}_i(u) < 0$, if $u > max\ \{K_1^*, K_2^*\}$ and $\mathrm{G}_i(u) > 0$, if $0 < u < min\ \{K_1^*, K_2^*\}$. Thus the positive unique steady-state solution u of (2.7) is respectively concave or convex on connected subsets of

$$\{s \in (0, L_2) : s \neq 0, L_1, L_2;\ u(s) > max\ \{K_1^*, K_2^*\}\}$$
or
$$\{s \in (0, L_2) : s \neq 0, L_1, L_2;\ 0 < u(s) < min\ \{K_1^*, K_2^*\}\}$$

Hence the unique solution u of (2.7) satisfies

$$min\ \{K_1^*, K_2^*\} \leq u(s) \leq max\ \{K_1^*, K_2^*\}$$

We now consider without loss of generality $0 < K_1^* < K_2^*$. Therefore $K_1^* \leq u \leq K_2^*$.

Let $p_i(s, \alpha_i)$, $L_{i-1} \leq s \leq L_i$, are the unique solution of the equation (2.7), for i=1,2 and $p_i(s, \alpha_i)$ are such that

$$\frac{\partial p_1}{\partial s}(0, \alpha_1) = \alpha_1, \quad p_1(0, \alpha_1) = K_1^*,$$
$$\frac{\partial p_2}{\partial s}(L_2, \alpha_2) = \alpha_2, \quad p_2(L_2, \alpha_2) = K_2^*.$$

Multiplying both sides of (2.7) by $2du_i/ds$, and integrating from 0 if i=1 and from L_2 if i=2, we get

$$\left[\frac{du_i}{ds}\right]^2 - \alpha_i^2 = -\frac{2}{D_i} \int_{K_i^*}^{u_i(s)} \xi_i(s) \left[\mathrm{g}_i(\xi_i(s)) - \mathrm{p}_i(\xi_i(s))\right] d\xi_i \tag{2.10}$$

Using (2.10), we now prove the following lemmas.

Lemma 2.3.1 *If $\alpha_1 > 0$, then*

$$\frac{\partial p_1(s, \alpha_1)}{\partial s} > \alpha_1 \text{ on } 0 < s \leq L_1.$$

Proof: From (2.10) , we get,

$$\left[\frac{\partial p_1(s, \alpha_1)}{\partial s}\right]^2 = \alpha_1^2 - \frac{2}{D_1} \int_{K_1^*}^{p_1(s,\alpha_1)} \xi_1[\mathrm{g}_1(\xi_1) - \mathrm{p}_1(\xi_1)] d\xi_1 \tag{2.11}$$

since

$$\frac{\partial p_1(0, \alpha_1)}{\partial s} = \alpha_1 > 0 \text{ , } p_1(0, \alpha_1) = K_1^* \text{ ,}$$

then there exists $s_1 > 0$ such that $p_1(s, \alpha_1) > K_1^*$ on $0 < s < s_1$. If not, let $s_0, 0 < s_0 \leq L_1$, be the first positive value, if it exists, such that $p_1(s_0, \alpha_1) = K_1^*$. Then by the mean value theorem there exists $\bar{s}$ such that $0 < \bar{s} < s_0$ and $\partial p_1(\bar{s}, \alpha_1)/\partial s = 0$; that is,

$$\alpha_1^2 = \frac{2}{D_1} \int_{K_1^*}^{p_1(\bar{s},\alpha_1)} \xi_1[\mathrm{g}_1(\xi_1) - \mathrm{p}_1(\xi_1)] d\xi_1. \tag{2.12}$$

Now since $p_1(s,\alpha_1) > K_1^*$ for $0 < s \leq \bar{s}$ and from (2.2), we have, $\mathrm{g}_1(\xi_1) - \mathrm{p}_1(\xi_1) < 0$. Hence the right hand side of (2.12) is negative, giving a contradiction. Therefore $p_1(s,\alpha_1) > K_1^*$ and $\partial p_1(s,\alpha_1)/\partial s > 0$. Now, noting that $(\partial p_1(s,\alpha_1)/\partial s)^2$ is an increasing function of p_1, the lemma follows. ∎

Lemma 2.3.2 *If $0 < p_2 < K_2^*$ and $\alpha_2 > 0$, then*

$$\frac{\partial p_2(s,\alpha_2)}{\partial s} > \alpha_2, \quad L_1 \leq s < L_2.$$

Proof: From (2.10),we have,

$$\left[\frac{\partial p_2(s,\alpha_2)}{\partial s}\right]^2 = \alpha_2^2 - \frac{2}{D_2}\int_{K_2^*}^{p_2(s,\alpha_2)} \xi_2[\mathrm{g}_2(\xi_2) - \mathrm{p}_2(\xi_2)]d\xi_2$$

and since $0 < p_2 < K_2^*$, hence from (2.2), $\xi_2[\mathrm{g}_2(\xi_2) - \mathrm{p}_2(\xi_2)] > 0$. Hence $\partial p_2(s,\alpha_2)/\partial s > \alpha_2$, $L_1 \leq s < L_2$ for $0 < p_2 < K_2^*$. ∎

Lemma 2.3.3 *Define $F_i(\alpha_i)$ by $F_i(\alpha_i) = p_i(L_1,\alpha_i)$. Then there exists $\hat{\alpha}_i > 0$, such that*

$$F_1 \;:\; [0,\hat{\alpha}_1] \;\rightarrow\; [K_1^*,\; K_2^*]$$

$$F_2 \;:\; [0,\hat{\alpha}_2] \;\rightarrow\; [K_2^*,\; K_1^*]$$

Proof: Note that $F_i(\alpha_i)$, if it exists, is continuous. The existence of $\hat{\alpha}_1 > 0$ follows from the following, we note that $F_1(0) = K_1^*$, $F_1(\alpha_1) > K_1^*$ if $\alpha_1 > 0$ (by Lemma 2.3.1), and that $F_1(\infty) = \infty$. Hence we choose $\hat{\alpha}_i > 0$ to be the least value of α_1 such that $F_1(\hat{\alpha}_1) = K_2^*$.

To show that $\hat{\alpha}_2$ exists, we note that $F_2(0) = K_2^*$. By continuity, $F_2(\alpha_2)$ exists for sufficiently small α_2, $\alpha_2 > 0$. From Lemma 2.3.2, $F_2[(K_2^* - K_1^*)/(L_2 - L_1)]$ is either less than K_1^* or does not exist. Therefore, there exists at least an $\hat{\alpha}_2$, such that $\hat{\alpha}_2 = K_1^*$, hence the lemma. ∎

Theorem 2.3.2 *There exists a continuous, monotonic solution of system (2.7) with continuous flux at L_1.*

Proof: Lemmas 2.3.1 and 2.3.2 follow that any solution we construct must be monotonic. By Lemma 2.3.3, for each $0 \le \alpha_2 \le \hat{\alpha}_2$, we can find an α_1 such that $0 \le \alpha_1 \le \hat{\alpha}_1$ for which $p_1(L_1, \alpha_1) = p_2(L_1, \alpha_2)$. Hence α_1 can be solved as a function of α_2, $\alpha_1 = h(\alpha_2)$, to give a continuous solution of (2.7) with (2.8) and (2.10).

Let

$$\mathcal{G}(\alpha_2) = D_1 \frac{\partial p_1(L_1, h(\alpha_2))}{\partial s} - D_2 \frac{\partial p_2(L_1, \alpha_2)}{\partial s}$$

Clearly $\mathcal{G}(\alpha_2)$ is continuous on $0 \le \alpha_2 \le \hat{\alpha}_2$. Then we have

$$\mathcal{G}(0) = D_1 \frac{\partial p_1(L_1, \hat{\alpha}_1)}{\partial s} > 0,$$

and

$$\mathcal{G}(\hat{\alpha}_2) = -D_2 \frac{\partial p_2(L_1, \hat{\alpha}_2)}{\partial s} < 0.$$

Hence the theorem. ∎

Now we find the conditions for asymptotic stability of the non-uniform steady state in both linear and non-linear cases.

Theorem 2.3.3 *The steady-state, continuous, monotonic solution of the system (2.1), with continuous flux matching condition at the interface (2.3), and under reservoir boundary*

conditions (2.4), is locally asymptotically stable if

$$\frac{d}{du_2}\left(u_2[\mathbf{g}_2(u_2) - \mathbf{p}_2(u_2)]\right) < 0, \qquad K_1^* \le u_2 \le K_2^* \tag{2.13}$$

Proof: Linearizing (2.1) by using

$$N_i(s,t) = u_i(s) + n_i(s,t) \quad i = 1,2 \tag{2.14}$$

We have

$$\frac{\partial n_i(s,t)}{\partial t} = n_i\left[\mathbf{g}_i(u_i) + u_i\mathbf{g}_i'(u_i) - \mathbf{p}_i(u_i) - u_i\mathbf{p}_i'(u_i)\right] + D_i\frac{\partial^2 n_i}{\partial s^2} \tag{2.15}$$

Using (2.14), the corresponding reservoir boundary conditions and the matching conditions at the interface are as follows :

$$\begin{aligned} n_1(0,t) &= n_2(L_2,t) = 0 \\ n_1(L_1,t) &= n_2(L_1,t) \\ D_1\frac{\partial n_1}{\partial s}(L_1,t) &= D_2\frac{\partial n_2}{\partial s}(L_2,t) \end{aligned} \tag{2.16}$$

Now we consider the following positive definite function ($L_0 = 0$),

$$V(t) = \sum_{i=1}^{2}\int_{L_{i-1}}^{L_i}\frac{1}{2}n_i^2 ds \tag{2.17}$$

Differentiating (2.17) and using (2.15) and (2.16), we get

$$\begin{aligned} \dot{V}(t) &= \int_0^{L_1} n_1^2\left[\mathbf{g}_1(u_1) + u_1\mathbf{g}_1'(u_1) - \mathbf{p}_1(u_1) - u_1\mathbf{p}_1'(u_1)\right]ds + D_1\int_0^{L_1} n_1\frac{\partial^2 n_1}{\partial s^2}ds \\ &+ \int_{L_1}^{L_2} n_2^2\left[\mathbf{g}_2(u_2) + u_2\mathbf{g}_2'(u_2) - \mathbf{p}_2(u_2) - u_2\mathbf{p}_2'(u_2)\right]ds + D_2\int_{L_1}^{L_2} n_2\frac{\partial^2 n_2}{\partial s^2}ds \end{aligned}$$

Now, considering the following integral and using (2.16), we get

$$\begin{aligned} \mathcal{J} &= D_1\int_0^{L_1} n_1\frac{\partial^2 n_1}{\partial s^2}ds + D_2\int_{L_1}^{L_2} n_2\frac{\partial^2 n_2}{\partial s^2}ds \\ &= D_1 n_1(L_1,t)\frac{\partial n_1}{\partial s}(L_1,t) - D_2 n_2(L_1,t)\frac{\partial n_2}{\partial s}(L_1,t) \\ &\quad -D_1\int_0^{L_1}\left(\frac{\partial n_1}{\partial s}\right)^2 ds - D_2\int_{L_1}^{L_2}\left(\frac{\partial n_2}{\partial s}\right)^2 ds \\ &= -D_1\int_0^{L_1}\left(\frac{\partial n_1}{\partial s}\right)^2 ds - D_2\int_{L_1}^{L_2}\left(\frac{\partial n_2}{\partial s}\right)^2 ds \end{aligned} \tag{2.18}$$

Further since for $0 \leq s \leq L_1$, $u_1 \geq K_1^*$, $\mathbf{G}_1(u_1) = \mathbf{g}_1(u_1) - \mathbf{p}_1(u_1) < 0$, and $\mathbf{G}_1'(u_1) = \mathbf{g}_1'(u_1) - \mathbf{p}_1'(u_1) < 0$, the expression $\mathbf{g}_1(u_1) + u_1\mathbf{g}_1'(u_1) - \mathbf{p}_1(u_1) - u_1\mathbf{p}_1'(u_1)$ is negative.

Hence $\dot{V}(t)$ is negative definite if the condition (2.13) holds true, thus proving the theorem. ∎

Remark: For $L_1 \leq s < L_2$, $u_2 < K_2^*$, $\mathbf{G}_2(u_2) = \mathbf{g}_2(u_2) - \mathbf{p}_2(u_2) > 0$, and $\mathbf{G}_2'(u_2) < 0$. This implies that the expression in the third integral is negative for u_2 very close to K_2^*. Since it is smooth, it remain so $\forall\, u_2,\ \ K_1^* \leq u_2 < K_2^*$ by (2.13).

Finally we state and prove the nonlinear stability theorem.

Theorem 2.3.4 *The steady-state, continuous, monotonic solution of the system (2.1) with continuous flux matching condition at the interface (2.3), and under the reservoir boundary conditions (2.4), is non-linearly asymptotically stable in the subregion of $K_1^* \leq N_i, u_i \leq K_2^*$, for $i = 1, 2$, if,*

$$\frac{(N_i\mathbf{g}_i(N_i) - u_i\mathbf{g}_i(u_i))}{N_i - u_i} - \frac{(N_i\mathbf{p}_i(N_i) - u_i\mathbf{p}_i(u_i))}{N_i - u_i} \leq 0, \tag{2.19}$$

Proof: From (2.1), (2.7) and (2.14), we have

$$\frac{\partial n_i}{\partial t} = (N_i\mathbf{g}_i(N_i) - u_i\mathbf{g}_i(u_i)) - (N_i\mathbf{p}_i(N_i) - u_i\mathbf{p}_i(u_i)) + D_i\frac{\partial^2 n_i}{\partial s^2} \tag{2.20}$$

Now consider the same positive definite function as given in (2.17),

$$V(t) = \sum_{i=1}^{2}\int_{L_{i-1}}^{L_i}(N_i - u_i)^2 ds = \sum_{i=1}^{2}\int_{L_{i-1}}^{L_i} n_i^2 ds$$

Therefore,

$$\dot{V}(t) \;=\; \sum_{i=1}^{2}\int_{L_{i-1}}^{L_i} n_i^2\left[\frac{(N_i)\mathbf{g}_i(N_i) - u_i\mathbf{g}_i(u_i)}{N_i - u_i} - \frac{(N_i)\mathbf{p}_i(N_i) - u_i\mathbf{p}_i(u_i)}{N_i - u_i}\right] ds$$

$$+ \sum_{i=1}^{2} D_i \int_{L_{i-1}}^{L_i} n_i \frac{\partial^2 n_i}{\partial s^2} ds \tag{2.21}$$

and the second integral is always negative by (2.18).

Therefore $\dot{V}(t) \leq 0$ if the conditions (2.19) are satisfied. ∎

Remark: Using the mean value theorem,

$$\frac{(N_i)\mathrm{g}_i(N_i) - u_i\mathrm{g}_i(u_i)}{N_i - u_i} - \frac{(N_i)\mathrm{p}_i(N_i) - u_i\mathrm{p}_i(u_i)}{N_i - u_i} = \mathrm{g}_i(\xi_i) + \xi_i\mathrm{g}_i'(\xi_i) - \mathrm{p}_i(\xi_i) - \xi_i\mathrm{p}_i'(\xi_i) \tag{2.22}$$

where ξ_i is a fixed point for $i = 1, 2$, lies between N_i and u_i. Since $K_1^* \leq N_i, u_i \leq K_2^*$, therefore $K_1^* \leq \xi_i \leq K_2^*$. Again from (**H.1**), $\mathrm{p}_i(\xi_i) \geq 0$, $\mathrm{p}_i'(\xi_i) \geq 0$ and $\mathrm{g}_i'(\xi_i) \leq 0, \forall \xi_i \geq 0$. Also $\mathrm{g}_i(\xi_i) \leq 0$, only when $\xi_i \geq K_i$, therefore the conditions (2.19), for $i = 1$ is always true if both $u_1, N_1 \geq K_1 \geq K_1^*$. Further from (2.22) for $i = 1, 2$,

$$0 \geq -\xi_i\mathrm{g}_i'(\xi_i) + \mathrm{p}_i(\xi_i) + \xi_i\mathrm{p}_i'(\xi_i) \geq \mathrm{g}_i(\xi_i)$$

is the another form of the conditions (2.19).

2.3.2 Analysis under No-Flux Boundary Conditions

Similarly, we analyze the steady state solution under no-flux boundary conditions of our model (2.1), (2.3), (2.5), and (2.6). The steady state problem takes the form,

$$D_i \frac{d^2 u_i}{ds^2} + u_i\mathrm{g}_i(u_i) - u_i\mathrm{p}_i(u_i) = 0 \quad i = 1, 2 \tag{2.23}$$

The no-flux boundary conditions are given by

$$\frac{d}{ds}u_1(0) = 0 = \frac{d}{ds}u_2(L_2) \tag{2.24}$$

And at the interface $s = L_1$, we have

$$D_1 \frac{du_1(L_1)}{ds} = D_2 \frac{du_2(L_1)}{ds}, \quad u_1(L_1) = u_2(L_1) \tag{2.25}$$

Let $q_i(s,\beta_i)$, $L_{i-1} \le s \le L_i$, are the unique solutions of the equation (2.23), for i=1,2 and $q_i(s,\beta_i)$ are such that

$$\frac{\partial q_1}{\partial s}(0,\beta_1) = 0, \quad q_1(0,\beta_1) = \beta_1$$

$$\frac{\partial q_2}{\partial s}(L_2,\beta_2) = \beta_2, \quad q_2(L_2,\beta_2) = \beta_2$$

It may be noted here that it is possible to show the existence of a positive, monotonic, continuous with continuous flux solution, if we can show that there exist β_1, β_2 such that

$$D_1\frac{\partial q_1(L_1,\beta_1)}{\partial s} = D_2\frac{\partial q_2(L_1,\beta_2)}{\partial s}, \quad q_1(L_1,\beta_1) = q_2(L_1,\beta_2)$$

Multiplying both sides of (2.23) by $2du_i/ds$ and integrating from 0 if i=1 and from L_2 if i=2, we get

$$\left[\frac{du_i}{ds}\right]^2 = -\frac{2}{D_i}\int_{\beta_i}^{u_i(s)} \xi_{ii}\left[\mathrm{g}_i(\xi_i) - \mathrm{p}_i(\xi_i)\right] d\xi_i \tag{2.26}$$

By using (2.26), the following lemmas are proved analogous to their counterparts in the previous section.

Lemma 2.3.4 *If $\beta_1 > K_1^*$, then*

$$\frac{\partial p_1(s,\beta_1)}{\partial s} > 0 \ , \ 0 < s \le L_1$$

Proof: From (2.26), we get,

$$\left[\frac{\partial p_1(s,\beta_1)}{\partial s}\right]^2 = -\frac{2}{D_{11}}\int_{\beta_1}^{p_1(s,\beta_1)} \xi_1\left[\mathrm{g}_1(\xi_1) - \mathrm{p}_1(\xi_1)\right] d\xi_1 \tag{2.27}$$

Since $\partial p_1(0,\beta_1)/\partial s = 0$, $p_1(0,\beta_1) = \beta_1$ there exists $s_1 > 0$ such that $p_1(s,\beta_1) > \beta_1$ on $0 < s < s_1$. If not, let s_0, $0 < s_0 \le L_1$, be the least positive value , if it exists, such that $p_1(s_0,\beta_1) = \beta_1$. Then by the mean value theorem there exists $\bar{s}$ such that $0 < \bar{s} < s_0$ and

$\partial p_1(\bar{s}, \beta_1)/\partial s = 0$; that is,

$$0 = -\frac{2}{D_{11}} \int_{\beta_1}^{p_1(\bar{s},\beta_1)} \xi_1 \left[\mathbf{g}_1(\xi_1) - \mathbf{p}_1(\xi_1)\right] d\xi_1 \tag{2.28}$$

But the right hand side of (2.28) is non-zero, since $p_1(s, \beta_1) \neq \beta_1$ on $0 < s \leq \bar{s}$, giving a contradiction. Hence $p_1(s, \beta_1) > \beta_1$, for all value $0 < s \leq L_1$. Also $\beta_1 > K_1^*$, implies, $p(s, \beta_1) > K_1^*$, on $0 < s \leq L_1$. Hence by (2.2) and (2.27), the result follows. ∎

Lemma 2.3.5 *If $0 < p_2(s, \beta_2) \leq K_2^*$, then $\beta_2 < K_2^*$ which implies $p_2(s, \beta_2) < \beta_2$, for $L_1 \leq s < L_2$.*

Proof: Since $0 < p_2(s, \beta_2) \leq K_2^*$, then from (2.2), we get,

$$p_2\left[\mathbf{g}_2(p_2) - \mathbf{p}_2(p_2)\right] > 0$$

Now, since $\beta_2 < K_2^*$, then $p_2\mathbf{g}_2(p_2) - q_2\mathbf{p}_2(p_2) > 0$, $\forall\ \beta_2, p_2$. If possible let $p_2 > \beta_2$, then the right hand side of (2.26) is negative, which is impossible. Therefore $p_2(s, \beta_2) < \beta_2$. ∎

Lemma 2.3.6 *Define $\mathcal{H}_i(\beta_i)$, by $\mathcal{H}_i(\beta_i) = p_i(L_1, \beta_i)$, such that*

$$\mathcal{H}_1 \;:\; \left[K_1^*, \hat{\beta}_1\right] \;\rightarrow\; [K_1^*, K_2^*],$$

and

$$\mathcal{H}_2 \;:\; \left[\hat{\beta}_2, K_2^*\right] \;\rightarrow\; [K_1^*, K_2^*].$$

Proof: Since $p_i(L_1, \beta_i)$ is continuous function, therefore if $\mathcal{H}_i(\beta_i)$ exists, then it must be continuous. We choose $\mathcal{H}_1(K_1^*) = K_1^*$, this is possible since $p_1(0, K_1^*) = K_1^*$ and

$\partial p_1/\partial s(0, K_1^*) = 0$. Now from Lemma 2.3.4, $\mathcal{H}_1(\beta_1) > K_1^*$ if $\beta_1 > K_1^*$ and since $\mathcal{H}_1(\beta_1)$ is continuous, therefore $\mathcal{H}_1(\infty) = \infty$. Hence we can find $\hat{\beta}_1 > K_1^*$ to be the first value of β_1 such that $\mathcal{H}_1(\hat{\beta}_1) = K_2^*$.

Again, choose $\mathcal{H}_2(K_2^*) = p_2(L_2, K_2^*) = K_2^*$ and from Lemma 2.3.5, if $\beta_2 < K_2^*$, then $p_2(L_1, \beta_2) < \beta_2$, and hence $\mathcal{H}_1(\beta_2) < \beta_2 < K_2^*$. Then there exists $\hat{\beta}_2$ such that $\mathcal{H}_2(\hat{\beta}_2) = K_1^*$. Hence the result. ∎

Theorem 2.3.5 *There exists a continuous, monotonic solution of system (2.23) with continuous flux at L_1.*

Proof: By Lemma 2.3.6, for each $\hat{\beta}_2 \leq \beta_2 \leq K_2^*$, we can choose a β_1 such that $K_1^* \leq \beta_1 \leq \hat{\beta}_1$ for which $p_1(L_1, \beta_1) = p_2(L_1, \beta_2)$. Hence β_1 can be solved as a function of β_2 in the form $\beta_1 = f(\beta_2)$ to give a continuous solution of (2.23). We now define,

$$\mathcal{I}(\beta_2) = D_1 \frac{\partial p_1}{\partial s}(L_1, f(\beta_2)) - D_2 \frac{\partial p_2}{\partial s}(L_1, \beta_2). \tag{2.29}$$

Then

$$\mathcal{I}(\hat{\beta}_2) = -D_2 \frac{\partial p_2}{\partial s}(L_1, \hat{\beta}_2) < 0, \quad \mathcal{I}(K_2^*) = D_1 \frac{\partial p_1}{\partial s}(L_1, \hat{\beta}_1) > 0.$$

Now by continuity, there exists β_2, $\hat{\beta}_2 < \beta_2 < K_2^*$, such that $\mathcal{I}(\beta_2) = 0$.

Since $f(\beta_2) = \beta_1 > K_1^*$, Lemma 2.3.4 shows that our solution is monotonic on $0 \leq s \leq L_1$. By Lemma 2.3.5, we note that on $L_1 \leq s \leq L_2$, the solution $p_2(s, \beta_2) < \beta_2$. If $p_2(s, \beta_2)$ is not monotonic over this interval, then there exists $\bar{s}$, $L_1 < \bar{s} < L_2$, such that $\partial p_2(\hat{s}, \beta_2)/\partial s = 0$. But then, by (2.26), $u_2'(\bar{s}) > 0$, $u_2(\bar{s}) > \beta_2$, giving a contradiction. This proves the theorem. ∎

Finally, the stability conditions under no-flux boundary conditions are the same as in the case of reservoir boundary conditions and proofs are similar.

Theorem 2.3.6 *The steady-state, continuous, monotonic solution of the system (2.1) with continuous flux matching condition at the interface (2.3) and under the no-flux boundary conditions (2.5), is locally asymptotically stable if*

$$\frac{d}{du_2}\left(u_2[\mathrm{g}_2(u_2) - \mathrm{p}_2(u_2)]\right) < 0, \qquad K_1^* \leq u_2 \leq K_2^* \tag{2.30}$$

Theorem 2.3.7 *The steady-state, continuous, monotonic solution of the system (2.1) with continuous flux matching condition at the interface (2.3), and under the no-flux boundary conditions (2.5), is non-linearly asymptotically stable in the subregion of $K_1^* \leq N_i, u_i \leq K_2^*$, for $i = 1, 2$, if,*

$$\frac{(N_i \mathrm{g}_i(N_i) - u_i \mathrm{g}_i(u_i))}{N_i - u_i} - \frac{(N_i \mathrm{p}_i(N_i) - u_i \mathrm{p}_i(u_i))}{N_i - u_i} \leq 0, \tag{2.31}$$

Remark: The effect of harvesting is to decrease the equilibrium level and modify the conditions for stability (see [10]). It is to be noted further that harvesting enhances stability, see conditions (2.30) and (2.31).

2.3.3 The Case of Uniform Equilibrium State

We show that uniform steady state of the system (2.1) $\rightarrow$ (2.6) is globally asymptotically stable in the homogeneous habitat, under both set of boundary conditions. In our model, there is a uniform steady state $N(s,t) \equiv K,\ 0 \leq s \leq L_2,\quad t \geq 0$, where K is the common carrying capacity in both the patches.

Theorem 2.3.8 *Let $K_1^* = K_2^* = K$. Then the unique steady state solution to (2.7) and either (2.8) or (2.24), $N(s,t) = K$ is globally asymptotically stable.*

Proof: Let $V(N) = V(t)$ be the positive definite function about $N = K$, given by

$$V(N) = V(t) = \sum_{i=1}^{2} \int_{L_{i-1}}^{L_i} \left[N_i - K - K\ln\frac{N_i}{K}\right] ds$$

Differentiating with respect to t, and using (2.1) we get,

$$\dot{V}(t) = \sum_{i=1}^{2} \int_{L_{i-1}}^{L_i} \frac{(N_i - K)}{N_i} \{N_i \mathrm{g}_i(N_i) - N_i \mathrm{p}_i(N_i)\} \, ds + \sum_{i=1}^{n} D_i \int_{L_{i-1}}^{L_i} \frac{N_i - K}{N_i} \frac{\partial^2 N_i}{\partial^2 s} ds$$

Using (2.2), the first integral on right hand side becomes negative, for all values of $N_i \neq K$. Since under both set of boundary conditions,

$$\sum_{i=1}^{n} D_i \int_{L_{i-1}}^{L_i} \frac{N_i - K}{N_i} \frac{\partial^2 N_i}{\partial^2 s} ds = -\sum_{i=1}^{n} D_i \int_{L_{i-1}}^{L_i} \frac{K}{N_i^2} \left(\frac{\partial N_i}{\partial s}\right)^2 ds < 0$$

Hence $\dot{V}(N) < 0$, and $V(K) = 0$. Therefore $V(N)$ is negative definite over $N > 0$ with respect to $N = K$. Hence the theorem. ∎

Remark: On comparing the results of this section and the previous two sections, it can be concluded that the nonuniform steady state is not globally asymptotically stable due to patchiness of the habitat.

In the following section, we will show numerically the existence of the unsteady state solutions as well as the positive, monotonic, continuous steady state of reaction-diffusion system of equations with reservoir boundary condition and flux matching condition at the interface.

2.4 Numerical Examples

In this section we analyze our model (2.1), (2.3), (2.4) and (2.6) for the particular growth rate functions

$$\mathrm{g}_i(N_i) = r_i \left[1 - \frac{N_i}{K_i}\right] \quad \text{and } \mathrm{p}_i(N_i) = a_i N_i \tag{2.32}$$

numerically by using finite difference method. From (2.32) we get,

$$G_i(N_i) = \mathrm{g}_i(N_i) - \mathrm{p}_i(N_i) = r_i\left(1 - \frac{N_i}{\bar{K}_i}\right), \tag{2.33}$$

where

$$\bar{K}_i = \frac{r_i K_i}{r_i + a_i K_i}, \quad i = 1, 2.$$

Without loss of generality let $\bar{K}_1 \leq \bar{K}_2$. Our aim is to solve both unsteady state and steady state solutions of the system. First we study the unsteady state solutions of the following problem, in a two-patch habitat,

$$\frac{\partial N_i}{\partial t}(s,t) = r_i N_i(s,t)\left[1 - \frac{N_i(s,t)}{\bar{K}_i}\right] + D_i\frac{\partial^2 N_i}{\partial s^2}(s,t), \quad i = 1, 2, \tag{2.34}$$

with the initial and boundary conditions:

$$N_i(s,0) = \bar{K}_1 + \frac{\bar{K}_2 - \bar{K}_1}{L_2}s, \text{ and} \tag{2.35}$$

$$N_1(0,t) = \bar{K}_1, \quad N_2(L_2,t) = \bar{K}_2. \tag{2.36}$$

The continuity and flux matching conditions at the interface $s = L_1$ are given by

$$N_1(L_1,t) = N_2(L_2,t), \quad D_1\frac{\partial N_1}{\partial s}(L_1,t) = D_2\frac{\partial N_2}{\partial s}(L_1,t). \tag{2.37}$$

The corresponding steady state solution (distribution) for this is given by the following equation in $0 \leq s \leq L_2$,

$$D_i\frac{d^2 u_i}{ds^2} + r_i u_i\left[1 - \frac{u_i}{\bar{K}_i}\right] = 0, \quad i = 1, 2 \tag{2.38}$$

with the reservoir boundary conditions (2.36) and continuity and the flux matching conditions at the interfaces (2.37).

We numerically slove the system (2.32) to (2.38) for the unsteady and steady state solutions, with the stability conditions (2.13) and (2.19), in this case are given by,

$$u_2 \geq \frac{\bar{K}_2}{2}, \text{ for } \bar{K}_1 \leq u_2 \leq \bar{K}_2. \tag{2.39}$$

and for $i = 1, 2,$

$$N_i + u_i \geq \bar{K}_i, \text{ for } \bar{K}_1 \leq N_i, \; u_i \leq \bar{K}_2.$$

for linear and non-linear stability conditions respectively. These results various set of parameters in Fig.2.1 – Fig.2.5.

Fig.2.1 and Fig.2.2 show that the unsteady state solutions are monoton to s and t. From Fig.2.1 and 2.2 we further note that as t becomes large, uns tends to steady state solution for the set of parameters satisfying stability con and (2.40).

It is seen from Fig.2.3 - 2.5 that the steady state solution (distribution) is tonically increasing or decreasing from the starting point $\bar{K}_1$ to the final point also shows the effect of diffusion coefficients on the steady state distribution, for D_i, $i = 1, 2$ (i.e. $D_i \rightarrow 0$), the steady state distribution tends to the equilibri carrying capacity) level in the respective patches for all s except very close to the terface but for large D_i's its behavior is linear.

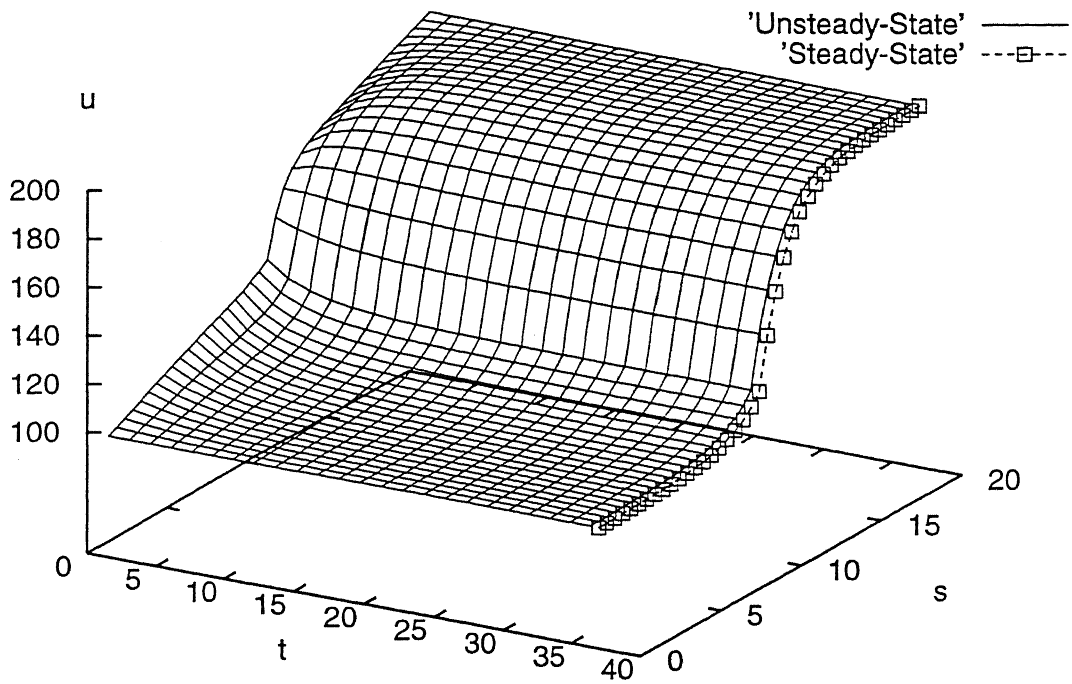


Figure 2.1: The unsteady state and steady state solutions, for $D_1 = 0.7$, $D_2 = 0.6$, $\bar{K}_1 = 100$, $\bar{K}_2 = 200$, $r_1 = 0.2$ and $r_2 = 0.3$

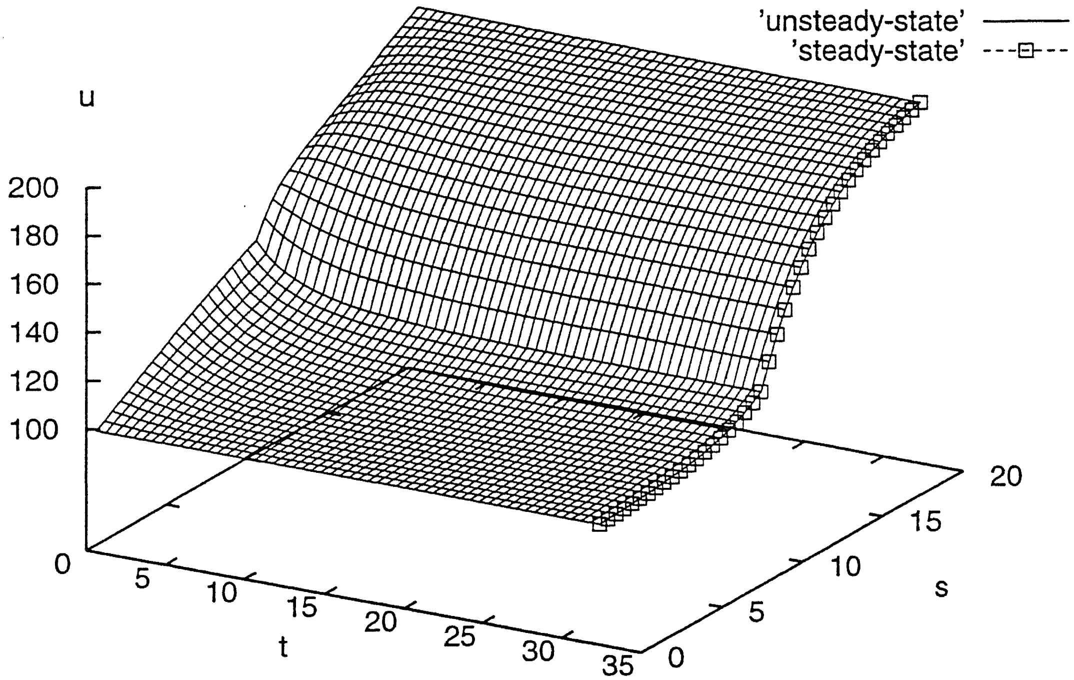


Figure 2.2: The unsteady state and steady state solutions, for $D_1 = 2.0$, $D_2 = 2.0$, $\bar{K}_1 = 100$, $\bar{K}_2 = 200$, $r_1 = 0.2$ and $r_2 = 0.2$

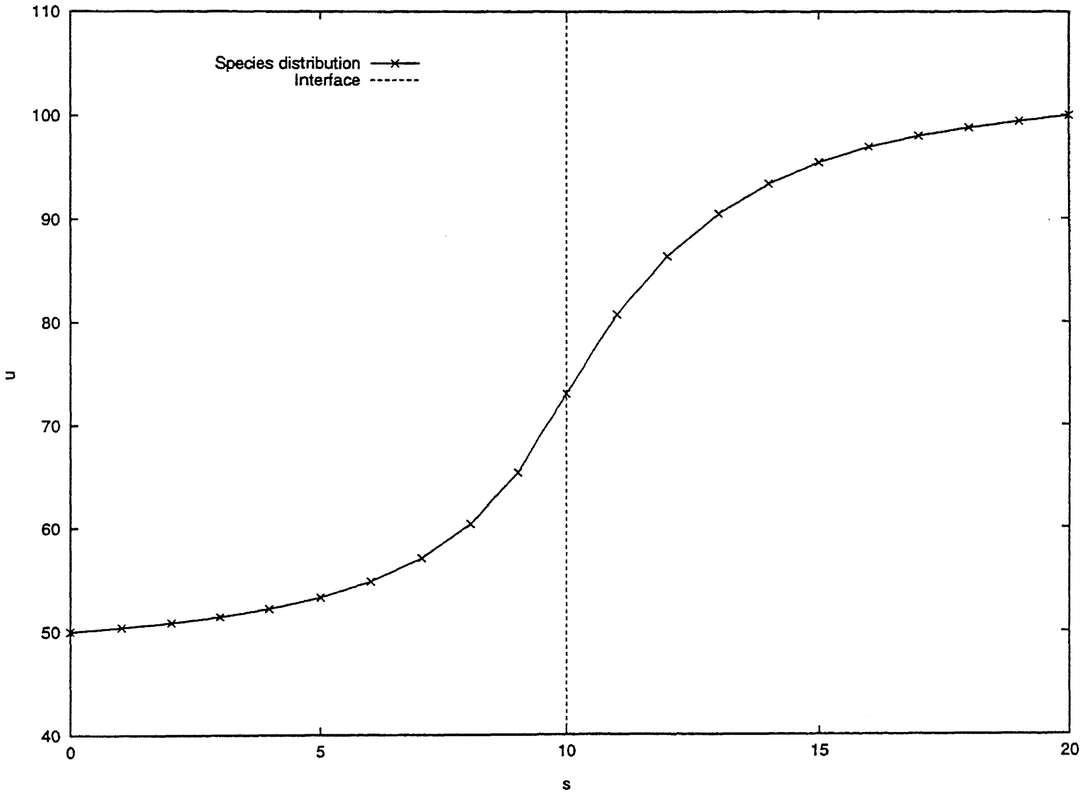


Figure 2.3: The steady state solution, when $\bar{K}_1 = 50 < \bar{K}_2 = 100$, for $D_1 = D_2 = 0.6$ and $r_1 = r_2 = 0.08$

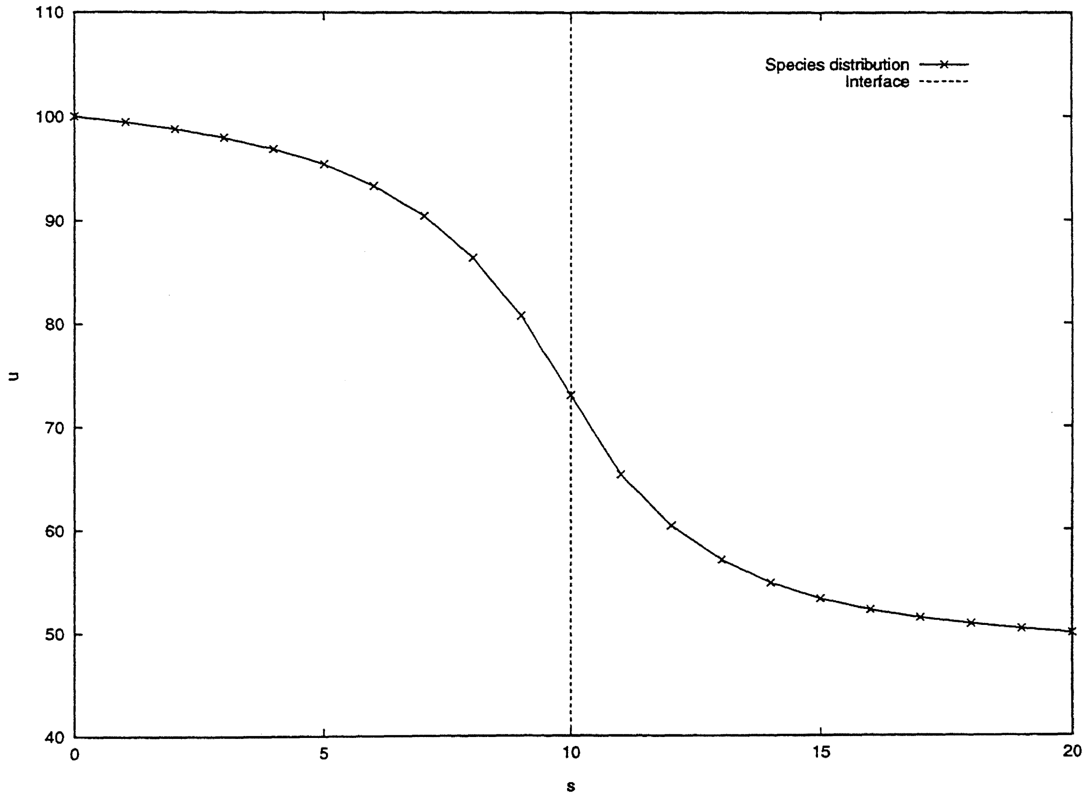


Figure 2.4: The steady state solution when $\bar{K}_1 = 100 > \bar{K}_2 = 50$, for $D_1 = D_2 = 0.6$ and $r_1 = r_2 = 0.08$

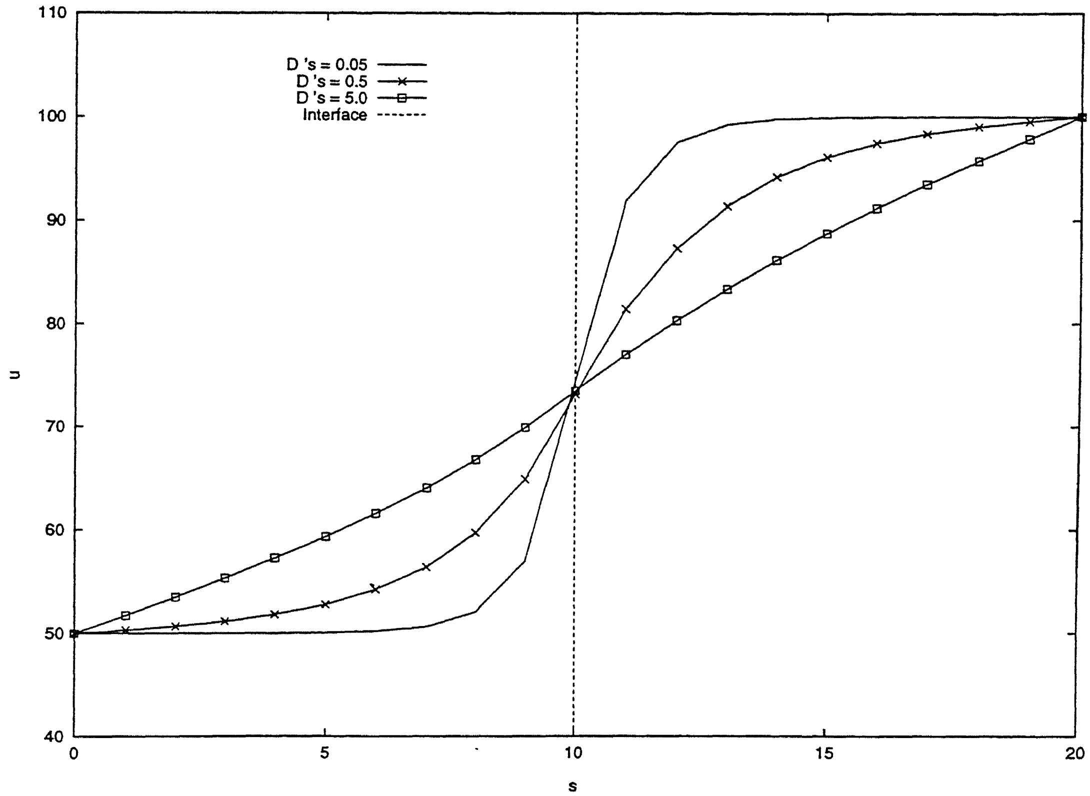


Figure 2.5: Effects of diffusion coefficients D_i's on the steady state distribution, when $\bar{K}_1 = 50 < \bar{K}_2 = 100$, for $r_1 = r_2 = 0.08$

2.5 Summary

A dynamical model of a single species population in a two patch habitats with harvesting and diffusion has been studied in this chapter. For application point of view, one may think of two adjoining forest stands whose carrying capacities are different due to deforestation, soil and other environmental conditions.

By analyzing the model, it has been shown that there exists a unique positive, monotonic, continuous steady state solution under both reservoir and no-flux boundary conditions. The stability of this non-uniform steady state is discussed for both linear and nonlinear cases. It is shown that the corresponding uniform steady state is globally asymptotically stable. Further, the comparison between the uniform and the non-uniform steady state solutions indicates that the patchiness decreases the stability of the system and the effect of harvesting is to decrease the level of equilibrium. These results are also proved by numerically solving the model under both steady and unsteady state conditions.

Bibliography

1. **Bailey, P., Shampine, L. F.**, and **Waltman, P. E.**, Nonlinear Two Point Boundary Value Problems, Academic, New York, 1968.

2. **Bernfeld, S. R.** and **Lakshmikantham, V.**, An Introduction to Nonlinear Boundary Value Problems, Academic, New York, 1974.

3. **Brown, W. K.**, Burawash uplands caribou herd: distribution and movement studies. *Report prepared for Foothill Pipelines (Yukon) Ltd. by Beak Consultants Ltd.*, Calgary (1981).

4. **Comins, H. N.** and **Blatt, D. W. E.**, Prey predator models in spatially heterogeneous environment, *J. Theor. Biol.*, Vol.**48**, 75-83 (1974).

5. **Freedman, H. I.**, Deterministic Mathematical Models in Population Ecology, HIFR Consulting Ltd., Edmonton, Canada (1987).

6. **Freedman, H. I.**, Single species migration in two habitats: persistence and extinction, *Math. Modelling*, Vol.**8**, 778-780 (1987).

7. **Freedman, H.I.** and **Krisztin, T.**, Global stability in models of population dynamics with diffusion. I. Patch environments, *Proc. Royal Soc. of Edinburgh*, Vol.**122A**, 69-84 (1992).

8. **Freedman, H. I., Rai, B.** and **Waltman, P.**, Mathematical models of population interactions with dispersal **II**: differential survival in a change of habitat, *J. Math. Anal. & Appl.*, Vol.**32**(3), (1977).

9. **Freedman,H.I.** and **Shukla,J.B.**, The effect of a predator resource on a diffusive predator-prey system, *Natural Resources Modeling*, Vol.**3**(3), 359-383, (1989).

10. **Freedman, H. I., Shukla, J. B.** and **Takeuchi,Y.**, Population diffusion in a two-patch environment, *Math. Biosci.*, Vol.**95**, 111-123, (1989).

11. **Freedman, H. I.** and **Waltman, P.**, Mathematical models of population interactions with dispersal I: stability of two habitats with and without a predator, *SIAM J. Appl. Math.*, Vol.**32**(3), (1977).

12. **Freedman, H.I.** and **Wu, J.B.**, Steady-State Analysis in a Model for Population Diffusion in a Multi-Patch Environment, *Nonl. Anal., Theor., Methods & Appl.*, Vol.**18**(6), 517-542, (1992).

13. **Gopalsamy, K.**, Competition, dispersion and co-existence, *Math. Bio. Sci.*, Vol.**33**, 25-33, (1977).

14. **Hastings, A.**, Dynamics of a Single Species in a Spatially Varying Environment: The Stabilizing Role of High Dispersal Rates, *J. Math. Biol.*, Vol.**16**, 49-55 (1982).

15. **Levin, S.A.**, Spatial patterning and the structure of ecological communities., Lectures on Mathematics in the Life Sciences, Vol.8,(1976).

16. **Nallaswamy, R.** and **Shukla, J.B.**, Effects of convective and dispersive migration on the linear stability of a two species system with mutualistic interactions and functional response, *Bul. Math. Biol.*, Vol.**44**, 271-282, (1982).

17. **Okubo, A.**, Diffusion and Ecological Problem: Mathematical models. Springer-Verlag, Berlin Heidelberg New York (1980).

18. **Rothe, F.**, Global Solution of Reaction Diffusion Systems, Springer-Verlag, Berline, Heidelberg, New York, Tokyo, (1984).

19. **Shukla, J.B.**, **Freedman, H.I.**, **Pal, V.N.**, **Mishra, O.P.**, **Agarwal, M.** and **Shukla, A.**, Degradation and subsequent regeneration of a resource: A mathematical model, *Ecol. Modelling*, Vol.**44**, 219-229, (1989).

20. **Shukla, J.B.** and **Verma, S.**, Effect of convective and dispersive interactions on the stability of two species, *Bul. Math. Biol.*, Vol.**43**, 593-610, (1981).

Chapter 3

A Single Species Model with Diffusion and Supplementary Resource in Homogeneous and Two-patch Habitats

3.1 Introduction

Degradation of a forest habitat caused by industrialization, pollution and increasing population, is of great concern to all humankind. A typical example in this regard is the depletion of the forest resources in the Doon Valley located in the foot hills of Himalayas, Utter Pradesh, India. Here the depletion of forest has been caused mainly by limestone quarrying, paper and other wood based industries and associated population migration [12]. Recently Shukla et al. [15] have proposed a mathematical model for forest depletion caused by resource independent industrialization (population) by considering the spatial distribution of both the forest biomass as well as the density of industrialization. By studying the behavior of uniform steady state solution, they have shown that if industrialization increases without control, the forest biomass may not last long.

This study implies that when forest stand or land is used for industrialization distributed spatially, patchiness is caused in the forest habitat leading to resource depletion. Similarly, the associated population, distributed nonuniformly and dependent upon resource biomass, is also found to be causing patchiness. Therefore it is important to study the effect of patchiness on the growth and existence of diffusing populations. It is noted that little effort has been made to study such problems using mathematical models [2, 4, 5, 15], though there exist several studies related to population diffusion [1, 6, 7, 8, 9, 10, 11, 13, 14, 16]. Freedman et al. [4] studied a single species diffusion model by assuming that the habitat consists of two adjoining patches and shown that there exists a positive, monotonic, continuous non uniform steady state solution that is linear asymptotically stable under both reservoir and no-flux boundary conditions. Freedman and Kriszti [2] have also consider the same problem in three patch habitat and shown that the positive steady state solution is pice-wise monotonic.

Further, when resource is depleted in the forest habitat due to industrialization etc., the species survival is threatened. One must therefore also study the effect of explicit dependence of population on resource in both homogeneous and patchy habitats. In this regard, Freedman and Shukla [3] have studied the effect of an alternative resource of predator population on predator-prey systems by considering diffusion in a homogeneous habitat. They, however neither considered the effect of patchiness in the habitat nor the behavior of the non-uniform steady state solution of the system.

In this chapter, we therefore, study the effect of supplementary self-renewable resource on a single species population with diffusion in a two patch habitat. The aim here is to show qualitatively that nonuniform steady state distribution of the species population is positive, continuous and monotonic through out the habitat and the level of distribution is higher then the case without supplementary resource [4]. We also obtain the conditions for stability of the system in both linear and nonlinear cases.

3.2 Mathematical Model

We consider a linear forest habitat $0 \leq s \leq L_2$, consisting of two adjoining patches $L_{i-1} \leq s \leq L_i$, for $i = 1, 2$, where $L_0 = 0$ and L_1 is the interface of the two patch. Let $R_i(s,t)$ is the density of the nondiffusing self-renewable supplementary resource and $N_i(s,t)$, be the densities of the species population bilinearly dependent on $R_i(s,t)$, at location s and time t in the i-th patch, for $i = 1, 2$. It is assumed that $R_i(s,t)$ grows logistically in both these patches with the different intrinsic growth rates (r_i) and the same carrying capacity (C). Further we assume that the growth rates $g_i(N_i)$ of $N_i(s,t)$, $i = 1, 2$ is general logistic type, in absence of the supplementary resource and is different in each patch. Keeping in view of the above, the model governing the system can be written as follows:

$$\frac{\partial R_i}{\partial t} = r_i R_i (1 - \frac{R_i}{C}) - \beta_i R_i N_i \tag{3.1}$$

$$\frac{\partial N_i}{\partial t} = N_i g_i(N_i) + \theta_i \beta_i R_i N_i + D_i \frac{\partial^2 N_i}{\partial s^2} \tag{3.2}$$

$$\beta_i,\ \theta_i \geq 0, \quad 0 \leq s \leq L_2, \quad i = 1, 2.$$

where β_i and θ_i are respectively depletion rates of resource and the conversion rates of resource biomass in the corresponding patches and D_i are the diffusion coefficient of $N_i(s,t)$ in the i-th patch respectively, for $i = 1, 2$.

The growth rate $g_i(N_i)$ functions are such that
(H.1): $g_i(N_i) \in C^2[0,\infty)$, $g_i(0) > 0$, and $\forall N_i \geq 0$, $g_i'(N_i) \leq 0$.

We note that when the habitat has carrying capacity K_i in the i-th patch respectively, then $g_i(K_i) = 0$.

Further we assume that
(H.2): $\exists\ R_i^*, K_i^* > 0$ such that

$$g_i(K_i^*) + \theta_i \beta_i R_i^* = 0 \quad \text{and} \quad r_i(1 - \frac{R_i^*}{C}) - \beta_i K_i^* = 0.$$

The existence of (R_i^*, K_i^*) are shown by graphically in Fig.3.1 an it is noted from this figure that the equilibrium level of population increases as the level of supplementary resource density i.e. its carrying capacity increases. Further it is also clear both analytically and graphically, that $R_i^* \leq C$ and $K_i^* \geq K_i$.

The model (3.1), (3.2) is studied under both reservoir and no-flux boundary conditions separately. In reservoir boundary conditions, we assume,

$$N_1(0,t) = K_1^* \text{ and } N_2(L_2,t) = K_2^* \tag{3.3}$$

and in the case of no-flux boundary conditions, we have

$$\frac{\partial N_1(0,t)}{\partial s} = 0 = \frac{\partial N_2(L_2,t)}{\partial s} \tag{3.4}$$

To study the behavior of non-uniform solutions, we also assume the continuity and flux matching conditions for $N_i(s,t)$ at the interface $s = L_1$, $\forall\ t \geq 0$, as

$$N_1(L_1,t) = N_2(L_1,t), \quad D_1\frac{\partial N_1}{\partial s}(L_1,t) = D_2\frac{\partial N_2}{\partial s}(L_1,t) \tag{3.5}$$

Since the resource $R_i(s,t)$ is non-diffusing, these types of boundary and matching conditions are not required as there is no diffusion term in (3.1). It is further noted that at $s = L_1$, $R_i(s,t)$ will be continuous or discontinuous according as different levels of depletion rates in the two patches.

Finally the model is completed by assuming some positive initial distribution for both forest resource biomass density and population density, that is,

$$R_i(s,0) = \chi_i(s) > 0, \ L_{i-1} < s < L_i \tag{3.6}$$

$$N_i(s,0) = \delta_i(s) > 0, \ L_{i-1} < s < L_i \tag{3.7}$$

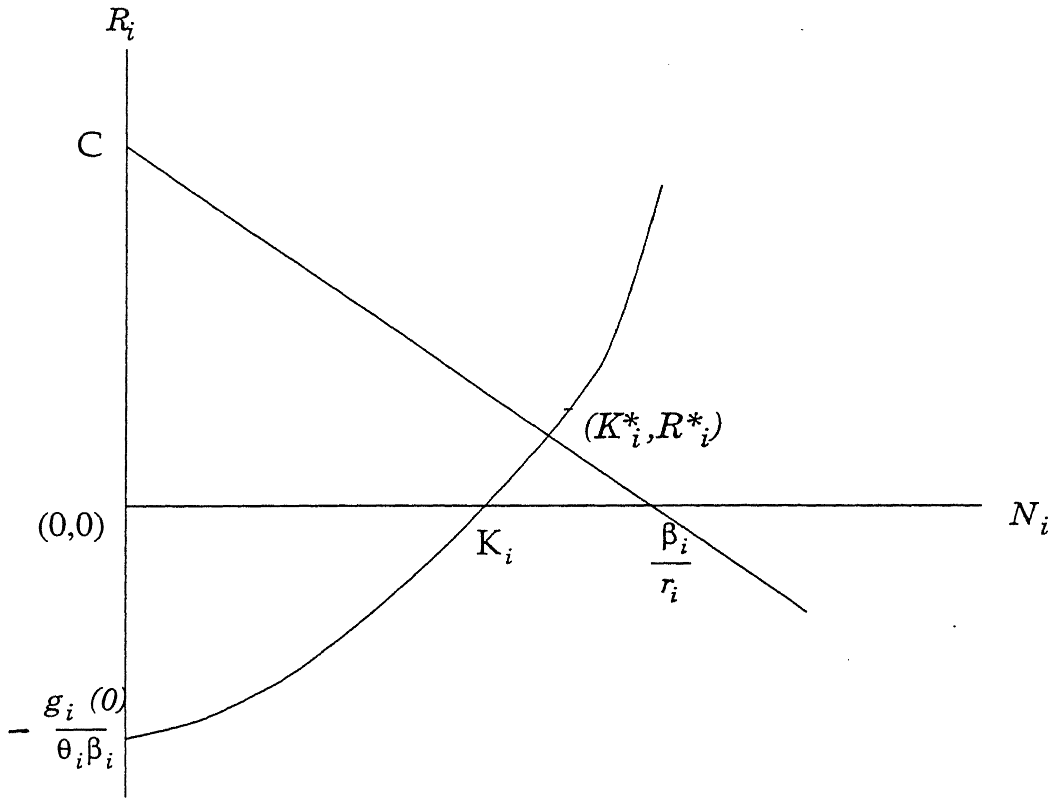


Figure 3.1: The existence of (R_i^*, K_i^*)

Our main aim is to study the behavior of the non-uniform steady state solutions of the above model, in the patch $0 \leq s \leq L_2$, as this will through light on the effect of supplementary resource on the species survival in the habitat.

Before we study our original model, in the following we state some important results for the corresponding model in a single homogeneous habitat $0 \leq s \leq L_2$ without and with diffusion.

3.3 Analysis of the Model in a Homogeneous Habitat

3.3.1 Model without Diffusion

In this case both the supplementary forest resource biomass and species population are uniformly distributed for all $0 \leq s \leq L_2$ without diffusion. Our model reduces to the following form:

$$\frac{dR}{dt} = rR(1 - \frac{R}{C}) - \beta RN \tag{3.8}$$

$$\frac{dN}{dt} = N\mathrm{g}(N) + \theta\beta RN \tag{3.9}$$

From equation (3.8) and (3.9) it follows that there are four equilibria, namely $E_0 = [0, 0]$, $E_C = [C, 0]$, $E_K = [0, K]$ and $E^* = [R^*, K^*]$, where R^*, K^*, from (3.8) and (3.9) are given by,

$$r(1 - \frac{R^*}{C}) - \beta K^* = 0, \text{ and } \mathrm{g}(K^*) + \theta\beta R^* = 0.$$

For $r > \beta K$, the existence of E^* is shown in Fig.3.1. It is also noted that, $R^* \leq C$ and $K^* \geq K$. The nature of R^* and K^* with respect to various parameters is shown in the table 3.1, which can be checked analytically.

Table 3.3: Effects of various parameters on R^* and K^*.

(i)	$r \uparrow$	$R^* \uparrow$	$K^* \uparrow$
(ii)	$a \uparrow$	$R^* \uparrow$	$K^* \downarrow$
(iii)	$C \uparrow$	$R^* \uparrow$	$K^* \uparrow$
(iv)	$K \uparrow$	$R^* \downarrow$	$K^* \uparrow$
(v)	$\theta \uparrow$	$R^* \downarrow$	$K^* \uparrow$
(vi)	$\beta \uparrow$ $R^* > C/2$	$R^* \downarrow$	$K^* \uparrow$

The notation $\uparrow$ and $\downarrow$ means increase and decrease respectively.

It is also observed that the most interesting interior (non-zero) equilibrium E^*, if it exists (i.e. $r > \beta K$), then by using the following positive definite functions,

$$V(R, N) = d(R - R^*)^2 + (N - K^*)^2, \tag{3.10}$$

$$V(N, R) = \left(R - R^* - R^* ln\frac{R}{R^*}\right) + \theta\left(N - K^* - K^* ln\frac{N}{K^*}\right) \tag{3.11}$$

where d and θ are positive constants, and by using Lyaponov direct method, we conclude that the equilibria E^* is locally as well as globally asymptotically stable for suitable choice of d and θ.

3.3.2 Model with Diffusion

Now we study the behavior of the uniform steady state solution of the model (3.1) - (3.7) with diffusion in a homogeneous habitat. Here $R_i(s,t)$, $N_i(s,t)$, α_i, K_i, D_i and β_i become $R(s,t)$, $N(s,t)$, a, K D and β respectively, $\forall s \in [0, L_2]$. Then the model in this case can be written as,

$$\frac{\partial R}{\partial t} = rR(1 - \frac{R}{C}) - \beta RN \tag{3.12}$$

$$\frac{\partial N}{\partial t}(s,t) = Ng(N) + \theta\beta RN + D\frac{\partial^2 N}{\partial s^2}(s,t) \tag{3.13}$$

$$0 \leq \theta \leq 1, \quad \beta \geq 0, \quad 0 \leq s \leq L_2.$$

The boundary and initial conditions are respectively,

$$N(0,t) = K^* = N(L_2,t) \quad \text{(reservoir boundary conditions)} \tag{3.14}$$

or

$$\frac{\partial N(0,t)}{\partial s} = 0 = \frac{\partial N(L_2,t)}{\partial s} \quad \text{(no-flux boundary conditions)} \tag{3.15}$$

and

$$R(s,0) = \chi(s) > 0, \; 0 < s < L_2 \tag{3.16}$$

$$N(s,0) = \delta(s) > 0, \; 0 < s < L_2 \tag{3.17}$$

It can be easily verified that by using the same positive definite functions as given in (3.10) and (3.11), the following theorem is true.

Theorem 3.3.1 *The uniform steady state of the system, i.e. (R^*, K^*) is locally as well as globally asymptotically stable if $r > \beta K$.*

Therefore if an equilibrium is stable in nondiffusing case it is always stable with diffusion. Hence there is no diffusion instability of the system.

Now we go for our original model, and study the behavior of the non-uniform steady state solutions of the system.

3.4 Analysis of the Model with Diffusion in a Two-Patch Habitat

3.4.1 The Non-Uniform Steady State under Reservoir Boundary Conditions

We consider the steady state problem of the system (3.1) - (3.7). Our aim is to show that there exists a non-uniform positive, continuous and monotonic steady state distribution

of the species population ($u_i(s)$) under reservoir boundary conditions and with continuous flux matching at the interface $s = L_1$. We will note later that the steady state distribution of the supplementary forest resource biomass ($w_i(s)$, $i = 1, 2$) in each patch of the habitat is positive, continuous and monotonic but there may exist a continuity or jump discontinuity at the interface $s = L_1$ according as the relation between growth rates and interaction coefficients. The steady-state system takes the form,

$$r_i w_i \left(1 - \frac{w_i}{C}\right) - \beta_i w_i u_i = 0 \tag{3.18}$$

$$D_i \frac{d^2 u_i}{ds^2} + u_i g_i(u_i) + \theta_i \beta_i w_i u_i = 0 \tag{3.19}$$

The reservoir boundary conditions are,

$$u_1(0, t) = K_1^*, \quad u_2(L_2, t) = K_2^*. \tag{3.20}$$

The continuous and the matching conditions at the interface are,

$$u_1(L_1) = u_2(L_1), \quad D_1 \frac{du_1}{ds}(L_1) = D_2 \frac{du_2}{ds}(L_1). \tag{3.21}$$

From (3.18), we can solve w_i as a function of u_i, as follows

$$w_i = C\left(1 - \frac{\beta_i}{r_i} u_i\right), \quad i = 1, 2. \tag{3.22}$$

From (3.22) it is clear that if u_i are continuously monotonically increasing (decreasing) then w_i are continuously monotonically decreasing (increasing) with continuity or discontinuity at the interface $s = L_1$, according as

$$\frac{\beta_1}{r_1} = \frac{\beta_2}{r_2}, \quad \text{or} \quad \frac{\beta_1}{r_1} \neq \frac{\beta_2}{r_2}. \tag{3.23}$$

Now by substituting the value of w_i from (3.22) in (3.19), we get

$$D_i \frac{d^2 u_i}{ds^2} + u_i G_i(u_i) = 0, \quad i = 1, 2 \tag{3.24}$$

where $\mathbf{G}_i(u_i) = \mathbf{g}_i(u_i) + \theta_i\beta_i C(1-\beta_i u_i/r_i)$, and $\mathbf{G}_i(0) > 0$, $\mathbf{G}_i'(u_i) \leq 0$, $\forall u_i \neq 0$. Therefore, for $i = 1, 2$, $\mathbf{G}_i(u_i)$ are logistic functions.

As in chapter 2, we can show that, there exists an unique steady state solution u of (3.24) satisfying,

$$min\ \{K_1^*, K_2^*\} \leq u(s) \leq max\ \{K_1^*, K_2^*\}$$

We now consider without loss of generality $0 < K_1^* \leq u_i \leq K_2^*$, $i = 1, 2$.

Let $p_i(s, \alpha_i)$, $L_{i-1} \leq s \leq L_i$, are the unique solution of the equation (3.24), for $i = 1, 2$, such that

$$\frac{\partial p_1}{\partial s}(0, \alpha_1) = \alpha_1, \quad p_1(0, \alpha_1) = K_1^*$$
$$\frac{\partial p_2}{\partial s}(L_2, \alpha_2) = \alpha_2, \quad p_2(L_2, \alpha_2) = K_2^*$$

To show the existence of the monotonic solutions it is sufficient to show that there exists α_1 and α_2 such that

$$p_1(L_1, \alpha_1) = p_2(L_1, \alpha_2), \quad D_1\frac{\partial p_1}{\partial s}(L_1, \alpha_1) = D_2\frac{\partial p_1}{\partial s}(L_1, \alpha_2)$$

Multiplying both side of (3.24) by $2du_i/ds$ and integrating from 0 if $i = 1$ and from L_2 if $i = 2$, we get

$$\left[\frac{du_i}{ds}\right]^2 = \alpha_i^2 - \frac{2}{D_i}\int_{K_i^*}^{u_i(s)} \xi_i \mathbf{G}_i(\xi_i) d\xi_i(s) \tag{3.25}$$

Hence by using equation (3.25) and proceeding in a similar manner as in the chapter 2, the following Lemma and Theorem can be proved.

Lemma 3.4.1 *If $\alpha_1 > 0$, then*

$$\frac{\partial p_1(s, \alpha_1)}{\partial s} > \alpha_1 \ on\ 0 < s \leq L_1.$$

Lemma 3.4.2 *If $0 < p_2 < K_2^*$ and $\alpha_2 > 0$, then*

$$\frac{\partial p_2(s,\alpha_2)}{\partial s} > \alpha_2, \quad L_1 \le s < L_2.$$

Lemma 3.4.3 *Define $F_i(\alpha_i)$ by $F_i(\alpha_i) = p_i(L_1, \alpha_i)$. Then there exists $\hat{\alpha}_i > 0$ such that*

$$F_1 \; : \; [0, \hat{\alpha}_1] \; \rightarrow \; [K_1^*, \; K_2^*]$$

$$F_2 \; : \; [0, \hat{\alpha}_2] \; \rightarrow \; [K_2^*, \; K_1^*]$$

Theorem 3.4.1 *There exists a continuous, monotonic solution u_i of speci with the no-flux boundary conditions (3.20) and continuous flux at L_1.*

Proof: From Lemmas 3.4.1 and 3.4.2, it follows that any solution we construct must be monotonic. By Lemma 3.4.3, for each $0 \le \alpha_2 \le \hat{\alpha}_2$, we can find an α_1 such that $0 \le \alpha_1 \le \hat{\alpha}_1$ for which $p_1(L_1, \alpha_1) = p_2(L_1, \alpha_2)$. Hence α_1 can be solved as a function of α_2, $\alpha_1 = h(\alpha_2)$, to give a continuous solution of (3.24) with (3.20) and (3.21).

Let

$$\mathbf{G}(\alpha_2) = D_1 \frac{\partial p_1(L_1, h(\alpha_2))}{\partial s} - D_2 \frac{\partial p_2(L_1, \alpha_2)}{\partial s}$$

Clearly $\mathbf{G}(\alpha_2)$ is continuous on $0 \le \alpha_2 \le \hat{\alpha}_2$. Then we have

$$\mathbf{G}(0) = D_1 \frac{\partial p_1(L_1, \hat{\alpha}_1)}{\partial s} > 0,$$

and

$$\mathbf{G}(\hat{\alpha}_2) = -D_2 \frac{\partial p_2(L_1, \hat{\alpha}_2)}{\partial s} < 0.$$

Hence the theorem.

Remark: From theorem 3.4.1 it is noted that if $K_1^* > K_2^*$ (or $K_1^* < K_2^*$) then the steady state solution u_i is monotonically increasing (or decreasing), for $0 \leq s \leq L_2$ and accordingly from (3.22) w_i is also continuously decreases (or increases) in both the patches, $0 \leq s < L_1$ and $L_1 \leq s \leq L_2$. Further the steady state distribution w_i of the renewable supplementary resource is continuous and monotonic at each point of both the patches but continuous or discontinuous at the interface of the two adjoining patches according as (3.23).

Now we find the conditions for asymptotic stability in both linear and non-linear case.

Theorem 3.4.2 *The steady-state continuous, monotonic solutions of system (3.1) and (3.2) with continuous solutions and flux at the interface $s = L_1$ is locally asymptotically stable if*

$$\mathcal{B}_i = g_i(u_i) + u_i g_i'(u_i) + \theta_i \beta_i w_i \leq 0 \tag{3.26}$$

and

$$\alpha_i{}^2[w_i - \theta_i u_i]^2 \leq 4\mathcal{A}_i\mathcal{B}_i \tag{3.27}$$

where

$$\mathcal{A}_i = r_i\left(1 - \frac{2w_i}{C}\right) - \beta_i u_i = -\frac{r_i w_i}{C} \leq 0, \quad \textit{for } i = 1, 2.$$

Proof : Let the steady-state solution of system (3.18) be

$$w(s) = \begin{cases} w_1(s), & 0 \leq s \leq L_1 \\ w_2(s), & L_1 \leq s \leq L_2 \end{cases}$$

And let the steady-state solution of system (3.19) be

$$u(s) = \begin{cases} u_1(s), & 0 \leq s \leq L_1 \\ u_2(s), & L_1 \leq s \leq L_2 \end{cases}$$

Lineariazing (3.1) and (3.2) by using,

$$R_i(s,t) = w_i(s) + m_i(s,t) \tag{3.28}$$

$$N_i(s,t) = u_i(s) + n_i(s,t) \tag{3.29}$$

We have,

$$\frac{\partial m_i}{\partial t} = m_i \left[r_i \left(1 - \frac{2w_i}{C} \right) - \beta_i u_i \right] - n_i \beta_i w_i \tag{3.30}$$

$$\frac{\partial n_i}{\partial t} = n_i \left[\mathrm{g}_i(u_i) + u_i \mathrm{g}_i'(u_i) + \theta_i \beta_i w_i \right] + m_i \theta_i \beta_i u_i + D_i \frac{\partial^2 n_i}{\partial s^2} \tag{3.31}$$

Using (3.28), the corresponding boundary and matching conditions can be obtained as follows

$$n_1(0,t) = K_1^*, \quad n_2(L_2,t) = K_2^* \tag{3.32}$$

$$n_1(L_1,t) = n_2(L_1,t), \quad D_1 \frac{\partial n_1}{\partial s}(L_1,t) = D_2 \frac{\partial n_2}{\partial s}(L_1,t) \tag{3.33}$$

Now we consider the following positive definite function,

$$V(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \frac{1}{2} \left[m_i^2 + n_i^2 \right] ds \tag{3.34}$$

from which we get,

$$\dot{V}(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \left[m_i \frac{\partial m_i}{\partial t} + n_i \frac{\partial n_i}{\partial t} \right] ds \tag{3.35}$$

By using (3.30), (3.31), (3.32) and (3.33), and integration by parts, we get,

$$\begin{aligned} \dot{V}(t) \; = \; & \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2 \mathcal{A}_i ds - \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i [\beta_i w_i - \theta_i \beta_i u_i] ds + \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2 \mathcal{B}_i ds \\ & - \sum_1^2 D_i \int_{L_{i-1}}^{L_i} \left[\frac{\partial n_i}{\partial s} \right]^2 ds \end{aligned} \tag{3.36}$$

where

$$\mathcal{A}_i = r_i \left(1 - \frac{2w_i}{C} \right) - \beta_i u_i \text{ and } \mathcal{B}_i = \mathrm{g}_i(u_i) + u_i \mathrm{g}_i'(u_i) + \theta_i \beta_i w_i$$

Again, by using (3.22), for $i = 1, 2$, we get

$$\mathcal{A}_i = -\frac{2r_i w_i}{C} + r_i \left(1 - \frac{\beta_i}{r_i} u_i \right) = -\frac{r_i w_i}{C} \leq 0 \tag{3.37}$$

and for $i = 1$,

$$\mathcal{B}_1 = \mathrm{g}_1(u_1) + u_1 \mathrm{g}_1'(u_1) + \theta_1 \beta_1 C \left(1 - \frac{\beta_1}{r_1} u_1 \right) \leq 0, \tag{3.38}$$

since $u_1 \geq K_1^* \geq K_1$, therefore $g_1(u_1) \leq 0$ and $g_1'(u_1) \leq 0$, $\forall\, u_1$. Hence the condition (3.38) is a very weak condition, later we will show in an example that for simple logistic function $g_1(u_1) = a_1(1 - u_1/K_1)$, the condition is automatically satisfied.

From (3.36) it is noted that $\dot{V}(t)$ is negative definite, if the conditions (3.26) and (3.27) are satisfied, for $i = 1, 2$.

In a similar manner, the following nonlinear stability result can be proved by using the same positive definite function as in theorem 3.4.2.
We consider the case, when $K_1^* \leq K_2^*$, then $R_1^* \geq R_2^*$.

Theorem 3.4.3 *The steady-state continuous, monotonic solutions of the nonlinear system (3.1) and (3.2) with continuous flux at the interface $s = L_1$ is asymptotically stable in the subregion of* $\mathbf{R}$: $\{R_2^* \leq R_i, w_i \leq R_1^*;\ \ K_1^* \leq N_i, u_i \leq K_2^*\}$, *provided the following conditions are satisfied:*

(i)
$$\mathcal{F}_{1i} = \frac{N_i g_i(N_i) - u_i g_i(u_i)}{N_i - u_i} + \theta_i \beta_i R_i \leq 0$$

(ii)
$$\mathcal{F}_{2i} = r_i \left(1 - \frac{R_i + w_i}{C}\right) - \beta_i N_i \leq 0$$

(iii)
$$\beta_i^2 \left[w_i - \theta_i u_i\right]^2 \leq 4\mathcal{F}_{1i}\mathcal{F}_{2i}$$

3.4.2 The Non-Uniform Steady State under No-Flux Boundary Conditions

In this section, consider the steady state problem of the system (3.18) and (3.19) with no-flux boundary condition,

$$\frac{du_1}{ds}(0) = 0 = \frac{du_2}{ds}(L_2) \tag{3.39}$$

and continuity and flux matching conditions at the interface (3.21).

In this case also, there exists a non-uniform positive, continuous and monotonic steady state distribution of the species population density ($u_i(s)$) and the steady state distribution of the supplementary resource biomass ($w_i(s)$, $i = 1, 2$) in each patch of the habitat is positive, continuous and monotonic but it may be continuous or discontinuous at the interface $s = L_1$, because of the following relation,

$$w_i = C\left(1 - \frac{\beta_i}{r_i}u_i\right), \quad i = 1, 2. \tag{3.40}$$

and the condition (3.23).

In this case also, it is clear from the above that if u_i are continuously monotonically increasing (decreasing) then w_i are continuously monotonically decreasing (increasing) with continuity or discontinuity at the interface $s = L_1$, according as (3.23).

After substituting the value of w_i from (3.40) in (3.19), we get

$$D_i \frac{d^2 u_i}{ds^2} + u_i \mathrm{G}_i(u_i) = 0, \quad i = 1, 2 \tag{3.41}$$

where $\mathrm{G}_i(u_i) = \mathrm{g}_i(u_i) + \theta_i \beta_i C(1 - \beta_i u_i / r_i)$.

Let $p_i(s, \beta_i)$, $L_{i-1} \leq s \leq L_i$, are the unique solutions of (3.41), for i = 1,2, such that

$$\frac{\partial p_1(0, \beta_1)}{\partial s} = 0 \quad , \quad p_1(0, \beta_1) = \beta_1 \tag{3.42}$$

$$\frac{\partial p_2(L_2, \beta_2)}{\partial s} = 0 \quad , \quad p_2(L_2, \beta_2) = \beta_2 \tag{3.43}$$

The existence of the monotonic solutions follows, if we can show that there exist β_1 and β_2, such that

$$p_1(L_1, \beta_1) = p_2(L_1, \beta_2) \;, \; D_1 \frac{\partial p_1(L_1, \beta_1)}{\partial s} = D_2 \frac{\partial p_2(L_1, \beta_2)}{\partial s} \tag{3.44}$$

From (3.41), multiplying both side by $2du_i/ds$ and then integrating with respect to s from 0 if $i = 1$ and from L_2 if $i = 2$, we get

$$\left[\frac{du_i}{ds}\right]^2 = -\frac{2}{D_i}\int_{\beta_i}^{u_i(s)} [\xi_i \mathbf{G}_i(\xi_i)]\, d\xi_i(s) \tag{3.45}$$

Then by exactly in similar manner as in previous section, we can state the following theorem.

Theorem 3.4.4 *There exists a continuous, monotonic solution u_i of species population with the no-flux boundary conditions (3.39) and continuous flux at L_1.*

We now state the linear and non-linear asymptotic stability theorems of the non-uniform steady state solutions of the system (3.18), (3.19) with (3.39) and (3.21) by using the Lyaponov direct method.

Theorem 3.4.5 *The steady-state continuous, monotonic solutions of system (3.1) and (3.2) with continuous solutions and flux at the interface $s = L_1$ is locally asymptotically stable if*

$$\mathcal{B}_i = \mathrm{g}_i(u_i) + u_i \mathrm{g}_i'(u_i) + \theta_i \beta_i w_i \leq 0 \tag{3.46}$$

and

$$\alpha_i{}^2[w_i - \theta_i u_i]^2 \leq 4\mathcal{A}_i\mathcal{B}_i \tag{3.47}$$

where

$$\mathcal{A}_i = r_i\left(1 - \frac{2w_i}{C}\right) - \beta_i u_i = -\frac{r_i w_i}{C} \leq 0, \quad \textit{for } i = 1, 2.$$

Proof: Same as Theorem 3.4.2 and only difference is in the condition (3.32), which becomes now,

$$\frac{\partial n_1}{\partial s}(0,t) = 0 = \frac{\partial n_2}{\partial s}(L_2,t) \quad . \tag{3.48}$$

In a similar manner, the following nonlinear stability result can be proved by using positive definite function as in theorem 3.4.3, for $K_1^* \leq K_2^*$.

Theorem 3.4.6 *The steady state continuous, monotonic solutions of nonlinear system with continuous flux at the interface $s = L_1$ is asymptotically stable in the subregion of* $\mathbf{R}$*: $\{R_2^* \leq R_i, w_i \leq R_1^*;\ \ N_1^* \leq N_i, u_i \leq N_2^*\}$, provided the following conditions are satisfied:*

(i)
$$\mathcal{F}_{1i} = \frac{N_i g_i(N_i) - u_i g_i(u_i)}{N_i - u_i} + \theta_i \beta_i R_i \leq 0$$

(ii)
$$\mathcal{F}_{2i} = r_i \left(1 - \frac{R_i + w_i}{C}\right) - \beta_i N_i \leq 0$$

(iii)
$$\beta_i^2 \left[w_i - \theta_i u_i\right]^2 \leq 4\mathcal{F}_{1i}\mathcal{F}_{2i}$$

The above theorems imply that the system will settle down to the steady state distribution in the two patches under certain conditions, the magnitude of the steady state distribution of resources biomass density being lower than it's original value but the density distribution of population being correspondingly higher in each patch.

3.4.3 The Uniform Steady State under Both Sets of Boundary Conditions

Now we consider the case when the species population is uniformly distributed between $[0, L_2]$, i.e. when $N_1(s,t) = N_2(s,t) = I^*$, $\forall\ s \in [0, L_2]$ and $\forall\ t \geq 0$. Since the depletion of supplementary resource $(R_i(s,t))$ due to population is different in different patch, i.e. $\beta_1 \neq \beta_2$. Let $R_1(s,t) = R_1^*$, $0 \leq s < L_1$, $\forall\ t \geq 0$ and $R_2(s,t) = R_2^*$, $L_1 < s \leq L_2$, $\forall\ t \geq 0$. Without loss of generality, we choose $\beta_2 > \beta_1$, this implies from (3.22) that $R_1^* > R_2^*$. Now we go for the globally stability of the system.

Theorem 3.4.7 *If $u_1 = u_2 = I^*$, $w_1 = R_1^*$ and $w_2 = R_2^*$, Then the system is globally asymptotically stable.*

Proof: Let $V(x,y)$ be the positive definite function about $R_i = R_i^*$, $N_i = I^*$, given by

$$V(x,y) = \sum_1^2 \theta_i \int_{L_{i-1}}^{L_i} \left(R_i - R_i^* - R_i^* ln\frac{R_i}{R_i^*}\right) ds + \sum_1^2 \int_{L_{i-1}}^{L_i} \left(N_i - I^* - I^* ln\frac{N_i}{I^*}\right) ds \quad (3.49)$$

Differentiating (3.49) with respect to t, and using (3.1) and (3.2) we get,

$$\begin{aligned} \dot{V}(s,t) &= \sum_1^2 \int_{L_{i-1}}^{L_i} (R_i - R_i^*)^2 \left[-\frac{r\theta_i}{C}\right] ds + \sum_1^2 \int_{L_{i-1}}^{L_i} (N_i - I^*)^2 \left[-\frac{\alpha_i}{K_i}\right] ds \\ &+ \sum_1^2 D_i \int_{L_{i-1}}^{L_i} \frac{N_i - I^*}{N_i} \frac{\partial^2 N_i}{\partial s^2} ds \end{aligned} \quad (3.50)$$

Since under both set of boundary conditions,

$$[x_1(0,t) - K^*]\frac{\partial x_1}{\partial s}(0,t) = [x_2(L_2,t) - K^*]\frac{\partial x_2}{\partial s}(L_2,t) = 0 \quad (3.51)$$

Then by using (3.51), we get

$$\sum_1^2 D_i \int_{L_{i-1}}^{L_i} \frac{N_i - I^*}{N_i} \frac{\partial^2 N_i}{\partial s^2} ds = -\sum_1^2 D_i \int_{L_{i-1}}^{L_i} \frac{I^*}{N_i^2} \left(\frac{\partial N_i}{\partial s}\right)^2 ds \quad (3.52)$$

Hence from (3.50) and (3.51), $\dot{V} < 0$ $\forall R_i \neq R_i^*$, $\forall N_i \neq I^*$, and $\dot{V}(R_i^*, I^*) = 0$. Therefore $\dot{V}(R_i, N_i)$ is negative definite, proving the theorem. ∎

It may be remarked from the above nonlinear steady state analysis for non-uniform and uniform cases that patchiness destablizing the system, we can see by comparing the statement of the theorem 3.4.7 with theorem 3.4.2, and theorem 3.4.3 or theorem 3.4.5 and theorem 3.4.6.

3.5 A Particular Case

For clarity and simplification, we consider an example by takeing $g_i(N_i) = a_i\,(1 - N_i/K_i)$. Then the corresponding system can be written as,

$$\frac{\partial R_i}{\partial t} = r_i R_i (1 - \frac{R_i}{C}) - \beta_i R_i N_i \tag{3.53}$$

$$\frac{\partial N_i}{\partial t} = a_i N_i\,(1 - N_i/K_i) + \theta_i \beta_i R_i N_i + D_i \frac{\partial^2 N_i}{\partial s^2} \tag{3.54}$$

the existence of non-negative equilibrium (R^*, K^*) is given by,

$$R_i^* = \frac{\alpha_i C(r_i - \beta_i K_i)}{r\alpha_i + \beta_i^2 \theta_i C K_i},\quad K_i^* = \frac{r_i K_i(\alpha_i + \beta_i \theta_i C)}{r_i \alpha_i + \beta_i^2 \theta_i C K_i},\quad \text{provided } r_i > \beta_i K_i.$$

From above it is clear that $R_i^* \leq C$ and $K_i^* \geq K_i$. This shows that the effect of supplementary resource is to increase the equilibrium level of the species population. Also we note that in absence of interaction (i.e. $\beta_i = 0$), $R_1^* = R_2^* = C$, the biomass is uniformly distributed in the entire habitat.

The model is completed by taking same boundary, matching and initial conditions as in the general case (3.3) $\rightarrow$ (3.7).

Exactly in a similar as in the general case we study the above system (3.53) and (3.54) with (3.3) $\rightarrow$ (3.7) in both homogeneous habitat ($0 \leq s \leq L_2$) without and with diffusion and in two patch habitat.

3.5.1 Analysis of the Model in a Homogeneous Habitat

Case 1: **Model without diffusion:**

In this case both the supplementary forest resource biomass and species population are uniformly distributed for all $0 \leq s \leq L_2$. Our model reduces to the following form:

$$\frac{dR}{dt} = rR(1 - \frac{R}{C}) - \beta RN \tag{3.55}$$

$$\frac{dN}{dt} = aN(1 - \frac{N}{K}) + \theta\beta RN \tag{3.56}$$

From equation (3.55) and (3.56) it follows that there are four equilibria, namely $E_0 = [0, 0]$, $E_C = [0, C]$, $E_K = [K, 0]$ and $E^* = [R^*, K^*]$, where

$$R^* = \frac{aC(r - \beta K)}{ra + \beta^2\theta CK}, \quad K^* = \frac{rK(a + \beta\theta C)}{ra + \beta^2\theta CK}, \quad \text{provided } r > \beta K. \tag{3.57}$$

It is also noted from (3.57) that, $R^* \leq C$ and $K^* \geq K$.

The variational matrix of the system is given by

$$[M] = \begin{bmatrix} r\,(1 - 2R/C) - \beta N & -\beta R \\ \theta\beta N & a\,(1 - 2N/K) - \theta\beta R \end{bmatrix} \tag{3.58}$$

From (3.58) and the standard stability theory, we note the following obvious observations. The equilibria E_0 is always unstable. The equilibrium points E_C and E_K are stable or saddle point according as $a + \theta\beta C$ and $r - \beta K$ are negative or positive respectively. It is also observed that the most interesting interior (non-zero) equilibria E^* is locally stable, if it exists (i.e. $r > \beta K$).

Alternatively if $r > \beta K$, by using the same positive definite functions as in (3.10) and (3.11), and by using Lyaponov direct method, we conclude that the equilibria E^* is locally as well as globally asymptotically stable.

Case 2: **Model with diffusion:**

Now we study the behavior of the uniform steady state solution of the model (3.53) - (3.54) with diffusion in a single homogeneous habitat. In this case we consider that both the populations are spatially distributed. Here $R_i(s,t)$, $N_i(s,t)$, α_i, K_i, D_i and β_i becomes $R(s,t)$, $N(s,t)$, a, K D and β respectively, $\forall s \in [0, L_2]$. Then the model in this case can be written as,

$$\frac{\partial R}{\partial t} = rR(1 - \frac{R}{C}) - \beta RN \tag{3.59}$$

$$\frac{\partial N}{\partial t}(s,t) = aN(1-\frac{N}{K}) + \theta\beta RN + D\frac{\partial^2 N}{\partial s^2}(s,t) \tag{3.60}$$
$$0 \le \theta \le 1, \quad \beta \ge 0, \quad 0 \le s \le L_2.$$

The boundary and initial conditions are respectively,

$$N(0,t) = K^* = N(L_2,t), \text{ or } \frac{\partial N(0,t)}{\partial s} = 0 = \frac{\partial N(L_2,t)}{\partial s} \tag{3.61}$$

and

$$R(s,0) = \chi(s) > 0, \ 0 < s < L_2, \ \text{ and } N(s,0) = \delta(s) > 0, \ 0 < s < L_2 \tag{3.62}$$

It can be easily verified that under same positive definite functions given in (3.10) and (3.11), the following theorem is true,

Theorem 3.5.1 *The uniform steady state of the system, i.e. (R^*, K^*) is locally as well as globally asymptotically stable if $r > \beta K$.*

Therefore if an equilibrium is stable in nondiffusing case it is always stable with diffusion.

Now we go for our original model (3.53), (3.54), and study the behavior of the non-uniform steady state solutions of the system.

3.5.2 Analysis of the Model with Diffusion in a Two-Patch Habitat

Case 1: **Analysis under Reservoir Boundary Conditions**

Consider the following steady state system,

$$r_i w_i \left(1 - \frac{w_i}{C}\right) - \beta_i w_i u_i = 0 \tag{3.63}$$

$$D_i \frac{d^2 u_i}{ds^2} + \alpha_i u_i \left(1 - \frac{u_i}{K_i}\right) + \theta_i \beta_i w_i u_i = 0 \tag{3.64}$$

with (3.20) and (3.21).

Again from (3.63), we can solve w_i as a function of u_i, as follows

$$w_i = C\left(1 - \frac{\beta_i}{r_i} u_i\right), \quad i = 1, 2. \tag{3.65}$$

From (3.65) it is clear that if u_i are continuously monotonically increasing (decreasing) then w_i are continuously monotonically decreasing (increasing) with continuity or discontinuity at the interface $s = L_1$, according as

$$\frac{\beta_1}{r_1} = \frac{\beta_2}{r_2}, \quad \text{or} \quad \frac{\beta_1}{r_1} \neq \frac{\beta_2}{r_2}. \tag{3.66}$$

Now by substituting the value of w_i from (3.65) in (3.64), we get

$$D_i \frac{d^2 u_i}{ds^2} + C_i u_i \left(1 - \frac{u_i}{K_i^*}\right) = 0, \quad i = 1, 2 \tag{3.67}$$

where $C_i = \alpha_i + \theta_i \beta_i C$.

Exactly as same in general case (chapter 2), there exists an unique steady state solution u of (3.67), which satisfies

$$min\ \{K_1^*, K_2^*\} \leq u(s) \leq max\ \{K_1^*, K_2^*\}$$

We now consider without loss of generality $0 < K_1^* \leq u_i \leq K_2^*$.

Let $p_i(s, \alpha_i)$, $L_{i-1} \leq s \leq L_i$, are the unique solution of the equation (3.67), for i=1,2. And $p_i(s, \alpha_i)$ are such that

$$\frac{\partial p_1}{\partial s}(0, \alpha_1) = \alpha_1, \quad p_1(0, \alpha_1) = K_1^*$$

$$\frac{\partial p_2}{\partial s}(L_2, \alpha_2) = \alpha_2, \quad p_2(L_2, \alpha_2) = K_2^*$$

Multiplying both side of (3.67) by $2du_i/ds$ and integrating from 0 if i=1 and from L_2 if i=2, we get

$$\left[\frac{du_i}{ds}\right]^2 = \alpha_i^2 - \frac{2}{D_i}\int_{K_i^*}^{u_i(s)}\left[C_i\xi_i\left(1-\frac{\xi_i}{K_i^*}\right)\right]d\xi_i(s) \tag{3.68}$$

Hence by using (3.68), the following theorem holds.

Theorem 3.5.2 *There exists a continuous, monotonic solution u_i of species population with the no-flux boundary conditions (3.20) and continuous flux at L_1.*

Now we find the most interesting results, the conditions for asymptotic stability in both linear and non-linear cases.

Theorem 3.5.3 *The steady-state continuous, monotonic solutions of system (3.63) and (3.64) with continuous solutions and flux at the interface $s = L_1$ is locally asymptotically stable if*

$$K_1^* \le u_1 \le min.\left\{K_2^*,\ \frac{F_1 + (F_1^2 - 4E_1G_1)^{1/2}}{2E_1}\right\} \tag{3.69}$$

and

$$max.\left\{K_1^*,\ \frac{r_2K_2(\alpha_2+\theta_2\beta_2C)}{2\alpha_2r_2+\theta_2\beta_2^2CK_2},\ \frac{F_2-(F_2^2-4E_2G_2)^{1/2}}{2E_2}\right\} \le u_2 \le K_2^* \tag{3.70}$$

Proof : Let the steady state solution of system (3.63) be

$$w(s) = \begin{cases} w_1(s), & 0 \le s \le L_1 \\ w_2(s), & L_1 \le s \le L_2 \end{cases}$$

Also let the steady-state solution of system (3.64) be

$$u(s) = \begin{cases} u_1(s), & 0 \le s \le L_1 \\ u_2(s), & L_1 \le s \le L_2 \end{cases}$$

Lineariazing (3.1) and (3.2) by using,

$$R_i(s,t) = w_i(s) + m_i(s,t) \tag{3.71}$$

$$N_i(s,t) = u_i(s) + n_i(s,t) \tag{3.72}$$

We have,

$$\frac{\partial m_i}{\partial t} = m_i \left[r\left(1 - \frac{2w_i}{C}\right) - \beta_i u_i \right] - n_i \beta_i w_i \tag{3.73}$$

$$\frac{\partial n_i}{\partial t} = n_i \left[\alpha_i \left(1 - \frac{2u_i}{K_i}\right) + \theta_i \beta_i w_i \right] + m_i \theta_i \beta_i u_i + D_i \frac{\partial^2 n_i}{\partial s^2} \tag{3.74}$$

Using (3.71) and (3.72), the corresponding boundary and matching conditions can be obtained as follows0

$$n_1(0,t) = K_1^*, \quad n_2(L_2,t) = K_2^* \tag{3.75}$$

$$n_1(L_1,t) = n_2(L_1,t), \quad D_1 \frac{\partial n_1}{\partial s}(L_1,t) = D_2 \frac{\partial n_2}{\partial s}(L_1,t) \tag{3.76}$$

Now we consider the following positive definite function,

$$V(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \frac{1}{2} \left[m_i^2 + n_i^2 \right] ds, \tag{3.77}$$

from which we get,

$$\dot{V}(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \left[m_i \frac{\partial m_i}{\partial t} + n_i \frac{\partial n_i}{\partial t} \right] ds \tag{3.78}$$

By using (3.73), (3.74), (3.75) and (3.76), and integration by parts, we get,

$$\begin{aligned} \dot{V}(t) &= \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2 \mathcal{A}_i ds - \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i [\beta_i w_i - \theta_i \beta_i u_i] ds + \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2 \mathcal{B}_i ds \\ &\quad - \sum_1^2 D_i \int_{L_{i-1}}^{L_i} \left[\frac{\partial n_i}{\partial s} \right]^2 ds \end{aligned} \tag{3.79}$$

where

$$\mathcal{A}_i = r_i \left(1 - \frac{2w_i}{C}\right) - \beta_i u_i \text{ and } \mathcal{B}_i = \alpha_i \left(1 - \frac{2u_i}{K_i}\right) + \theta_i \beta_i w_i$$

Again, by using (3.65), for $i = 1, 2$, we get

$$\mathcal{A}_i = -\frac{r_i w_i}{C} < 0 \tag{3.80}$$

$$\mathcal{B}_i = (\alpha_i + \theta_i\beta_i C) - \left[\frac{\alpha_i + \theta_i\beta_i C}{N_i^*} + \frac{\alpha_i}{K_i}\right] u_i \tag{3.81}$$

Let

$$M_i = \alpha_i + \theta_i\beta_i C, \;\; \mathcal{N}_i = \frac{M_i}{K_i^*} + \frac{\alpha_i}{K_i}$$

Now from (3.81), we note that for $\mathcal{B}_i \leq 0$, we have

$$u_i \geq \frac{M_i}{\mathcal{N}_i} = \frac{r_i K_i(\alpha_i + \theta_i\beta_i C)}{2\alpha_i r_i + \theta_i\beta_i^2 C K_i}, \quad i = 1, 2 \tag{3.82}$$

Since $K_1^* \leq u_i \leq K_2^*$, it is clear from (3.82) that $u_1 \geq M_1/\mathcal{N}_1$ is automatically satisfied. Therefore this condition is required only for u_2, for $\mathcal{B}_2 \leq 0$.

From (3.79) it is noted that $\dot{V}(t)$ is negative definite, if (3.82) is satisfied along with the following condition, for $i = 1, 2$

$$\beta_i^2[w_i - \theta_i u_i]^2 \leq 4\mathcal{A}_i\mathcal{B}_i \tag{3.83}$$

Now from (3.83), by using (3.65) and solving for u_i, $i = 1, 2$, we get

$$K_1^* \leq \frac{F_i - (F_i^2 - 4E_iG_i)^{1/2}}{2E_i} \leq u_i \leq \frac{F_i + (F_i^2 - 4E_iG_i)^{1/2}}{2E_i} \leq K_2^* \tag{3.84}$$

where

$$E_i = \beta_i^2\left(\theta_i + \frac{\beta_i C}{r_i}\right)^2 + 4\beta_i\mathcal{N}_i, \; F_i = 2\beta_i\left(\theta_i + \frac{\beta_i C}{r_i}\right) C + 4(r_i\mathcal{N}_i + \beta_i K_i), \; G_i = \beta_i^2 C^2 + 4r_i K_i.$$

Since $K_1^* \leq u_i \leq K_2^*$, and by using (3.82), (3.84), we get the conditions (3.69) and (3.70). Hence the theorem. ∎

The following numerical example shows the feasibility of the conditions (3.69) and (3.70).

Example: Let

$$\begin{array}{lllll} r = 0.2, & \alpha_1 = 0.2, & \alpha_2 = 0.25, & \beta_1 = 0.002, & \beta_2 = 0.0025 \\ C = 1000, & K_1 = 40, & K_2 = 70, & \theta_1 = 0.2, & \theta_2 = 0.5 \end{array}$$

we get,

$K_1^* = 66.6667,$ $K_2^* = 78.1395$

$F_1 - (F_1^2 - 4E_1G_1)^{1/2}/2E_1 = 0.1098,$ $F_1 + (F_1^2 - 4E_1G_1)^{1/2}/2E_1 = 77295.45,$

$F_2 + (F_2^2 - 4E_2G_2)^{1/2}/2E_2 = 50648.8,$ $F_2 - (F_2^2 - 4E_2G_2)^{1/2}/2E_2 = 0.1146.$

Hence in this case, (3.69) and (3.70) becomes

$$K_1^* = 66.6667 \leq u_i \leq K_2^* = 78.1395, \quad i = 1, 2.$$

In a similar manner, the following nonlinear stability result can be proved by using positive definite function as in theorem 2.3, for $K_1^* \leq K_2^*$.

Theorem 3.5.4 *The steady state continuous, monotonic solutions of nonlinear system with continuous flux at the interface $s = L_1$ is asymptotically stable in the subregion of* $\mathbf{R}$: $\{R_2^* \leq R_i, w_i \leq R_1^*;\ \ N_1^* \leq N_i, u_i \leq N_2^*\}$, *provided the following conditions are satisfied:*

(i)
$$\mathcal{F}_{1i} = \alpha_i \left(1 - \frac{N_i + u_i}{K_i}\right) + \theta_i\beta_i R_i \leq 0$$

(ii)
$$\mathcal{F}_{2i} = r_i \left(1 - \frac{R_i + w_i}{C}\right) - \beta_i N_i \leq 0$$

(iii)
$$\beta_i^2 \left[w_i - \theta_i u_i\right]^2 \leq 4\mathcal{F}_{1i}\mathcal{F}_{2i}$$

Proof: By using (3.72) and (3.71) the nonlinear model (3.1) and (3.2), we get

$$\frac{\partial n_i}{\partial t} = n_i \left[\alpha_i \left(1 - \frac{N_i + u_i}{K_i}\right) + \theta_i\beta_i R_i\right] + m_i\theta_i\beta_i u_i + D_i \frac{\partial^2 n_i}{\partial s^2}, \tag{3.85}$$

$$\frac{\partial m_i}{\partial t} = m_i \left[r_i \left(1 - \frac{R_i + w_i}{C}\right) - \beta_i N_i\right] - n_i\beta_i w_i. \tag{3.86}$$

We consider the following positive definite function,

$$V(t)=\sum_{1}^{2}\int_{L_{i-1}}^{L_i}\frac{1}{2}\left[n_i^2+m_i^2\right]ds \tag{3.87}$$

from which we get,

$$\dot{V}(t)=\sum_{i=1}^{2}\int_{L_{i-1}}^{L_i}n_i^2\left[\alpha_i\left(1-\frac{N_i+u_i}{K_i}\right)+\theta_i\beta_iR_i\right]ds+\sum_{i=1}^{2}\int_{L_{i-1}}^{L_i}\beta_i\left(w_i-\theta_iu_i\right)ds$$
$$+\sum_{i=1}^{2}\int_{L_{i-1}}^{L_i}m_i^2\left[r_i\left(1-\frac{R_i+w_i}{C}\right)-\beta_iN_i\right]ds++\sum_{i=1}^{2}D_i\int_{L_{i-1}}^{L_i}n_i\frac{\partial^2 n_i}{\partial s^2}, \tag{3.88}$$

Hence $\dot{V}(t)$ is negative definite if the conditions (i), (ii) and (iii) holds.

Note: The conditions (i) and (ii) are always satisfied if,

$$\alpha_i\le min\left[\alpha_i\frac{N_i+u_i}{K_i}-\theta_i\beta_iR_i\right]\;\Rightarrow\;1\le\frac{2K_1^*}{K_i}-\frac{\theta_i\beta_i}{\alpha_i}R_1^*. \tag{3.89}$$

$$r_i\le min\left[r_i\frac{R_i+w_i}{C}+\beta_iN_i\right]\;\Rightarrow\;\frac{2R_2^*}{C}+\frac{\beta_i}{r_i}K_1^*\ge 1 \tag{3.90}$$

Now using (3.89) and (3.90), we get the condition (iii) is always satisfied if

$$\beta_i^2\left[R_1^{*2}+\theta_i{}^2K_2^{*2}-2\theta_iR_2^*K_1^*\right]\le 4\mathcal{GF}_{1i}\mathcal{GF}_{2i}\left[1-\frac{2K_1^*}{K_i}+\frac{\theta_i\beta_i}{\alpha_i}R_1^*\right]\left[1-\frac{2R_2^*}{C}-\frac{\beta_i}{r_i}K_1^*\right] \tag{3.91}$$

Hence the system is nonlinearly asymptotically stable if (3.89) $\rightarrow$ (3.91) are satisfied.

Case 2: **Analysis under No-Flux Boundary Conditions**

The same analysis and results as in reservoir case (i.e. Case 1), are true for no-flux boundary conditions also. Therefore the nonuniform steady state is positive, monotonic and the system is linearly as well as nonlinearly stable under same set of condition as in theorem 3.5.2, 3.5.3 and 3.5.4.

3.5.3 The Uniform Steady State under Both Sets of Boundary Conditions

Now we consider the case when the species population is uniformly distributed between $[0, L_2]$, i.e. when $N_1(s,t) = N_2(s,t) = I^*$, $\forall\ s \in [0, L_2]$ and $\forall\ t \geq 0$. Since the depletion of supplementary resource $(R_i(s,t))$ due to population is different in different patch, i.e. $\beta_1 \neq \beta_2$, let $R_1(s,t) = R_1^*$, $0 \leq s < L_1$, $\forall\ t \geq 0$ and $R_2(s,t) = R_2^*$, $L_1 < s \leq L_2$, $\forall\ t \geq 0$. Without loss of generality, we choose $\beta_2 > \beta_1$, this implies from (3.22) that $R_1^* > R_2^*$. Now we go for the globally stability of the system.

Theorem 3.5.5 *If $u_1 = u_2 = I^*$, $w_1 = R_1^*$ and $w_2 = R_2^*$, Then the system is globally asymptotically stable.*

Proof: Let $V(x,y)$ be the positive definite function about $R_i = R_i^*$, $N_i = I^*$, given by

$$V(x,y) = \sum_1^2 \theta_i \int_{L_{i-1}}^{L_i} \left(R_i - R_i^* - R_i^* ln\frac{R_i}{R_i^*} \right) ds + \sum_1^2 \int_{L_{i-1}}^{L_i} \left(N_i - I^* - I^* ln\frac{N_i}{I^*} \right) ds \quad (3.92)$$

Differentiating (3.92) with respect to t, and using (3.1) and (3.2) we get,

$$\begin{aligned} \dot{V}(s,t) &= \sum_1^2 \int_{L_{i-1}}^{L_i} (R_i - R_i^*)^2 \left[-\frac{r\theta_i}{C} \right] ds + \sum_1^2 \int_{L_{i-1}}^{L_i} (N_i - I^*)^2 \left[-\frac{\alpha_i}{K_i} \right] ds \\ &+ \sum_1^2 D_i \int_{L_{i-1}}^{L_i} \frac{N_i - I^*}{N_i} \frac{\partial^2 N_i}{\partial s^2} ds \end{aligned} \quad (3.93)$$

Since under both sets of boundary conditions,

$$[x_1(0,t) - K^*]\frac{\partial x_1}{\partial s}(0,t) = [x_2(L_2,t) - K^*]\frac{\partial x_2}{\partial s}(L_2,t) = 0 \quad (3.94)$$

Then by using (3.94), we get

$$\sum_1^2 D_i \int_{L_{i-1}}^{L_i} \frac{N_i - I^*}{N_i} \frac{\partial^2 N_i}{\partial s^2} ds = -\sum_1^2 D_i \int_{L_{i-1}}^{L_i} \frac{I^*}{N_i^2} \left(\frac{\partial N_i}{\partial s} \right)^2 ds \quad (3.95)$$

Hence from (3.93) and (3.94), $\dot{V} < 0$ $\forall R_i \neq R_i^*$, $\forall N_i \neq I^*$, and $\dot{V}(R_i^*,\ I^*) = 0$. Therefore $\dot{V}(R_i, N_i)$ is negative definite, proving the theorem. ∎

3.6 Numerical Examples

In this section we calculate and study, the numerical solution of the steady state solutions the above particular case (3.63) and (3.64) with reservoir boundary conditions, and compare the results with the case discussed in chapter 1, for the following three set of values of the parameters,

Parameters	Figure 3.2	Figure 3.3	Figure 3.4
D_1	0.6	0.6	0.6
D_2	0.7	0.7	0.7
a_1	0.08	0.08	0.08
a_2	0.08	0.08	0.08
K_1	100	50	50
K_2	50	100	100
r_1	0.4	0.4	0.4
r_2	0.8	0.8	0.6
C	40	40	40
β_1	0.0003	0.0003	0.0003
β_2	0.0006	0.0006	0.0006
θ	0.5	0.5	0.5

Using these values of parameters, we get

Parameters	Figure 3.2	Figure 3.3	Figure 3.4
K_1^*	106.9	53.6	53.6
K_2^*	57.18	113.72	113.3
R_1^*	36.79	38.39	38.39
R_2^*	38.28	36.58	35.46

The results are shown in Fig.3.2, 3.3, 3.4. It can be noted that, in presence of the supplementary resource the level of the steady state distributions are higher at each point of the habitat. Again, in Fig.3.4, we consider the case when $\beta_1/r_1 \neq \beta_2/r_2$, it is shown that the steady state distribution of the renewable supplementary resource has a discontinuity at the interface of the patches. But in the first two figures, since $\beta_1/r_1 = \beta_2/r_2$, hence, the resource is continuous at the interface.

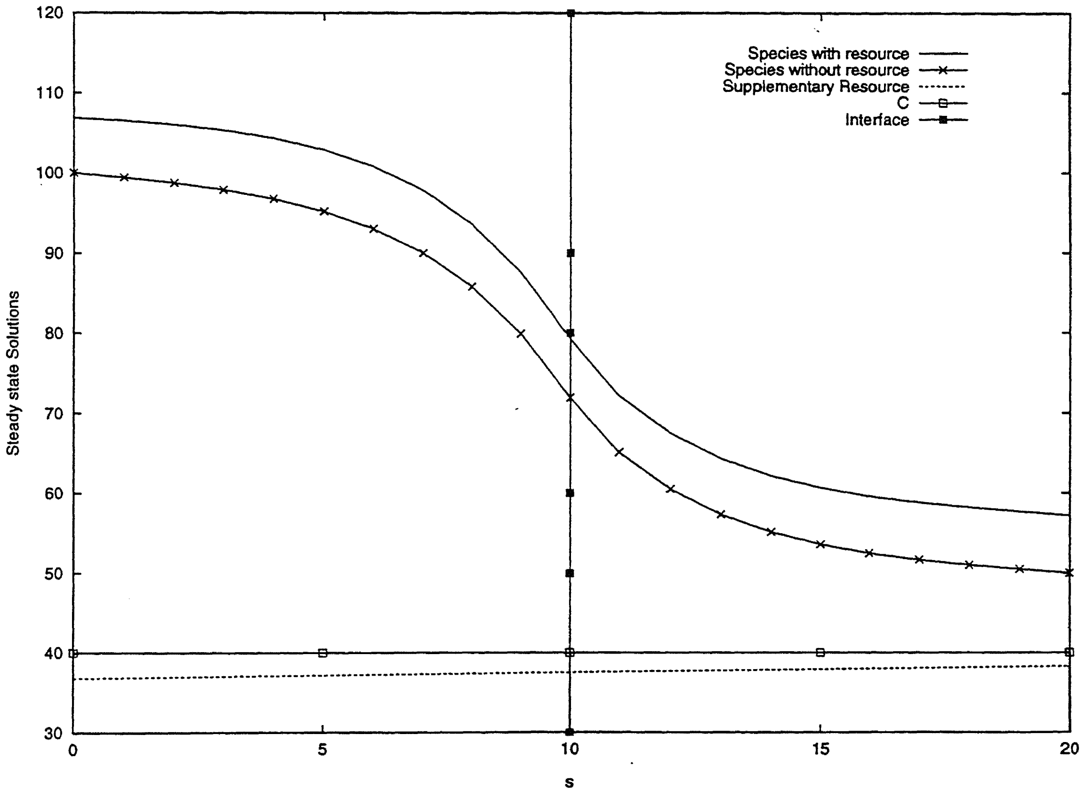


Figure 3.2: The steady state solutions, when $K_1^* > K_2^*$ and $\beta_1/r_1 = \beta_2/r_2$.

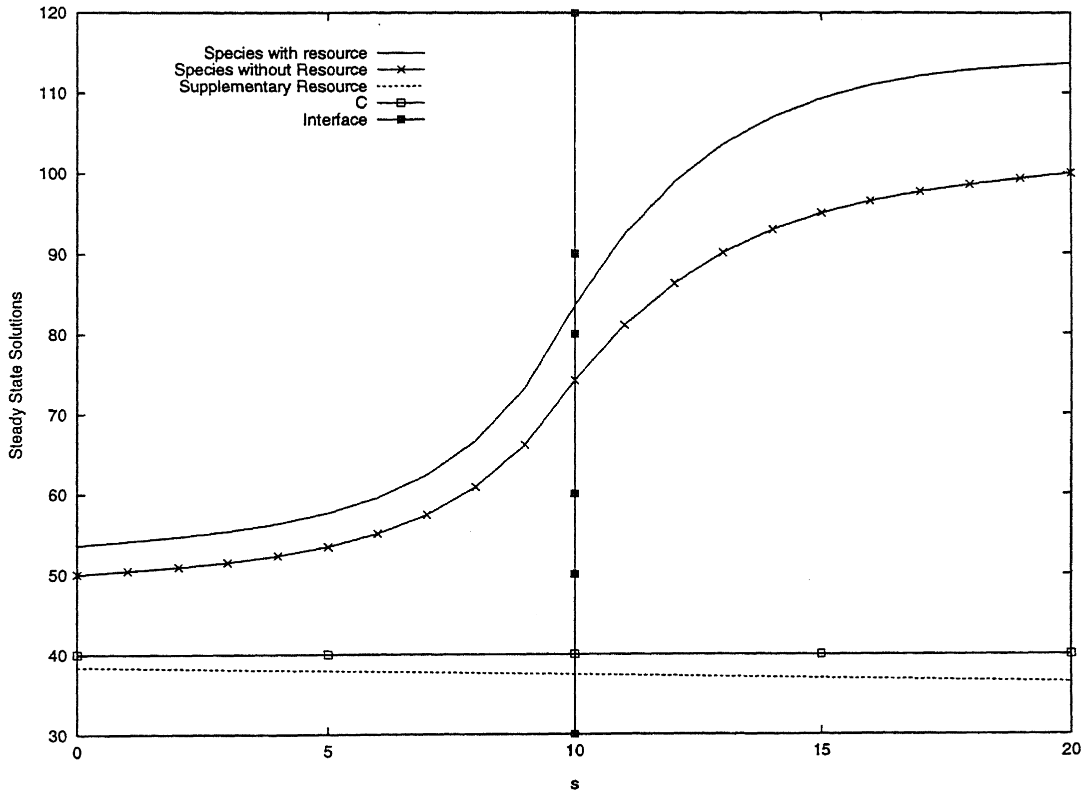


Figure 3.3: The steady state solutions, when $K_1^* < K_2^*$ and $\beta_1/r_1 = \beta_2/r_2$.

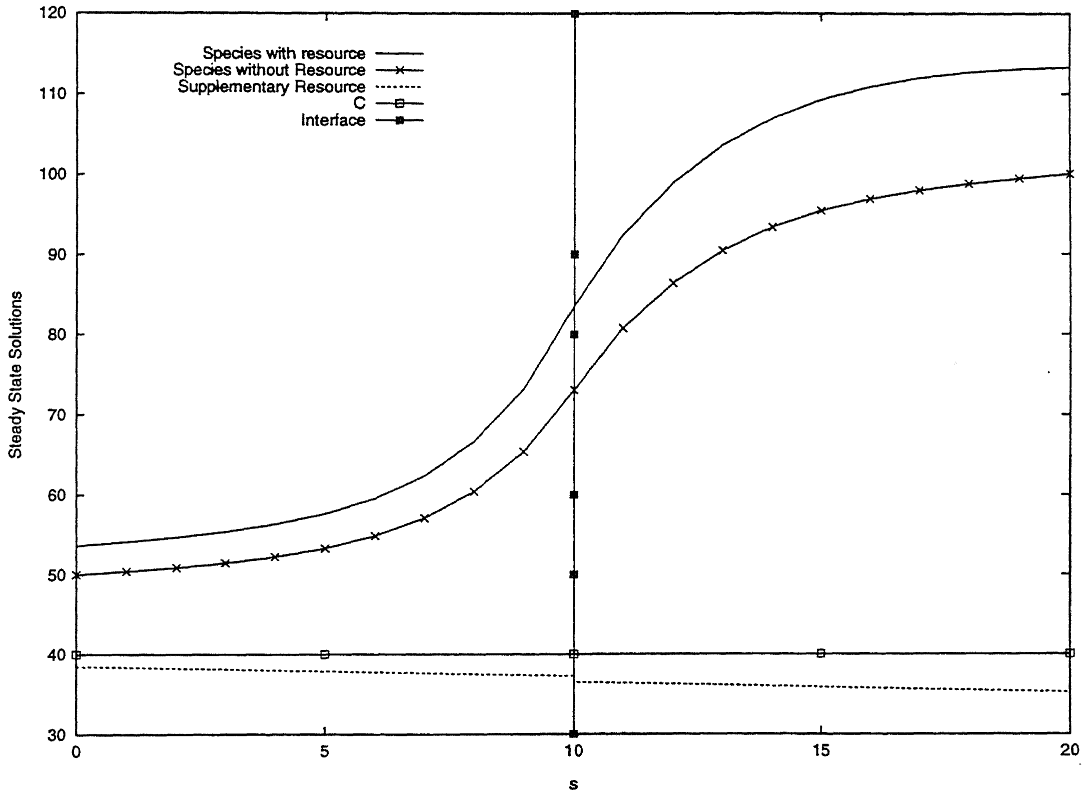


Figure 3.4: The steady state solutions, when $K_1^* < K_2^*$ and $\beta_1/r_1 \neq \beta_2/r_2$.

3.7 Summary

In this chapter, a mathematical model is proposed to study the role of supplementary renewable resource on a single species population model in a two patch habitat In the model it is assumed that the density of resource biomass is governed by the logistic equation with the different intrinsic growth rate but the same carrying capacity in the entire habitat. It is further assumed that the densities of species population is also governed by the logistic equations in both the patches but with different growth rates and carrying capacities. The rate of depletion of resource biomass density due to population is also considered to be different in the two patches.

It is shown that there exists a positive, monotonically increasing, continuous steady-state solution with continuous flux, in the case of both reservoir and no-flux boundary conditions, for both forest resource biomass and species population, that is asymptotically stable in the both linear and non linear cases under some conditions. It has been shown that forest resources remains at steady-state but at a lower level then it's carrying capacity the magnitude of which depends upon the level of population, but the marnitude of the steady state distribution of the population is always higher in presence of resource in comparison to the case of without resource. It is also noted that the patchiness in the habitat has a destablizing effect on the system.

Bibliography

1. **Comins, H.N., Blatt, D.W.E.**, *Prey predator models in spatially heterogeneous environment*, J. Theor. Biol.48, 75-83, (1974).

2. **Freedman, H.I.** and **Kriszti, T.**, *Global stability in model of population dynamics with diffusion.I. Patchy environment*, Proc. Royal Society of Edinburgh, 122A, 69-84, (1992).

3. **Freedman, H.I.** and **Shukla,J.B.**, *The effect of a predator resource on a diffusive predator-prey system*, Natural Resources Modeling, Vol.3(3), 359-383, (1989).

4. **Freedman, H.I., Shukla, J.B.** and **Takeuchi,Y.**, *Population diffusion in a two-patch environment*, Mathl. Biosc. 95, 111-123 (1989).

5. **Freedman, H.I.** and **Wu, J.**, *Steady state analysis in a model for population diffusion in a multi-patch environment*, Nonl. Anal., Theo., Meths. & Appl., Vol.18(6), 517-542, (1992).

6. **Hadeler, K.P., Heiden, V., Rothe, F.**, *Non-homogeneous spatial distributions of populations*, J. Math. Biol. 1, 165-176 (1974).

7. **Hastings, A.**, *Global stability in Lotka-Volterra systems with Diffusion*, J. Math. Biology 6, 163-168 (1978).

8. **Hastings, A.**, *Dynamics of a Single Species in a Spatially Varying Environment: The Stabilizing Role of High Dispersal Rates*, J. Math. Biol. 16, 49-55 (1982).

9. **Levin, S.A.**, *Population model and community structure in heterogeneous environments, in Mathematical Ecology*, T.G.Hallam and S.A.Levin,eds., Springer, New York, 295-321 (1986).

10. **Levin, S.A.**, *Dispersion and population interactions*, Am. Nat. 108, 207-228 (1974).

11. **McMurtrie, R.**, *Persistence and stability of single species and prey predator system in spatially heterogeneous environments*, Mathl. Biosc., 39: 11-51 (1978).

4.2 Mathematical Model

We consider a dynamic model of two logistically growing species with prey-predator type interaction and diffusion in a two-patch forest habitat by assuming that the second species (i.e. predator population) uses the first species (prey population) as an alternative resource. In such a case the rate of change of density of the first species decreases due increase in the density of the second species, but the density of the second species increases due to the increase in the density of the first species in both the patches. Let $x_i(s,t)$ and $y_i(s,t)$ be the densities of first and second species in the i-th patch respectively. Then the model can be written as the following system of autonomous partial differential equations:

$$\frac{\partial x_i(s,t)}{\partial t} = x_i(s,t)\mathrm{g}_i\left(x_i(s,t)\right) - y_i(s,t)\mathbf{p}_i\left(x_i(s,t)\right) + D_{1i}\frac{\partial^2 x_i(s,t)}{\partial s^2} \tag{4.1}$$

$$\frac{\partial y_i(s,t)}{\partial t} = y_i(s,t)\mathrm{f}_i\left(y_i(s,t)\right) + \gamma_i y_i(s,t)\mathbf{p}_i\left(x_i(s,t)\right) + D_{2i}\frac{\partial^2 y_i(s,t)}{\partial s^2} \tag{4.2}$$

$$0 \le s \le L_2, \quad i = 1,2, \quad \gamma_i \ge 0$$

where the i-th patch is assumed to lie along the spatial length $L_{i-1} \le s \le L_i$ $(L_0 = 0)$, $\mathrm{g}_i(x_i)$ and $\mathrm{f}_i(y_i)$ are the respective specific growth rates, $\mathbf{p}_i(x_i)$ is the interaction rates, and D_{1i} and D_{2i} are the diffusion coefficients of x_i and y_i in the two patches, $\gamma_i \ge 0$ be the growth rate coefficient of y_i due to x_i in the i-th patch respectively.

In writing the system (4.1) and (4.2) it is assumed that the growth rates and carrying capacities of two species are smaller or larger in the first patch than their corresponding values in the second patch depending upon whether the first patch is more or less depleted. Thus we assume $\mathrm{g}_i(x_i)$ and $\mathrm{f}_i(y_i)$ are logistic type functions and satisfying $\mathbf{H_1}$:

$\mathbf{H_1}$: $\mathrm{g}_i(x_i)$, $\mathrm{f}_i(y_i) \in \mathrm{C}^2[0,\infty)$

$\mathrm{g}_i(0) > 0$, for $x_i > 0$, $\mathrm{g}_i'(x_i) \le 0$,

$\mathrm{f}_i(0) > 0$, for $y_i > 0$, $\mathrm{f}_i'(y_i) \le 0$

$\mathrm{g}_i(K_i) = 0$, $\mathrm{f}_i(M_i) = 0$, $i = 1,2$.

3.7 Summary

In this chapter, a mathematical model is proposed to study the role of supplementary renewable resource on a single species population model in a two patch habitat In the model it is assumed that the density of resource biomass is governed by the logistic equation with the different intrinsic growth rate but the same carrying capacity in the entire habitat. It is further assumed that the densities of species population is also governed by the logistic equations in both the patches but with different growth rates and carrying capacities. The rate of depletion of resource biomass density due to population is also considered to be different in the two patches.

It is shown that there exists a positive, monotonically increasing, continuous steady-state solution with continuous flux, in the case of both reservoir and no-flux boundary conditions, for both forest resource biomass and species population, that is asymptotically stable in the both linear and non linear cases under some conditions. It has been shown that forest resources remains at steady-state but at a lower level then it's carrying capacity the magnitude of which depends upon the level of population, but the marnitude of the steady state distribution of the population is always higher in presence of resource in comparison to the case of without resource. It is also noted that the patchiness in the habitat has a destablizing effect on the system.

Bibliography

1. **Comins, H.N., Blatt, D.W.E.**, *Prey predator models in spatially heterogeneous environment*, J. Theor. Biol.48, 75-83, (1974).

2. **Freedman, H.I.** and **Kriszti, T.**, *Global stability in model of population dynamics with diffusion.I. Patchy environment*, Proc. Royal Society of Edinburgh, 122A, 69-84, (1992).

3. **Freedman, H.I.** and **Shukla,J.B.**, *The effect of a predator resource on a diffusive predator-prey system*, Natural Resources Modeling, Vol.3(3), 359-383, (1989).

4. **Freedman, H.I., Shukla, J.B.** and **Takeuchi,Y.**, *Population diffusion in a two-patch environment*, Mathl. Biosc. 95, 111-123 (1989).

5. **Freedman, H.I.** and **Wu, J.**, *Steady state analysis in a model for population diffusion in a multi-patch environment*, Nonl. Anal., Theo., Meths. & Appl., Vol.18(6), 517-542, (1992).

6. **Hadeler, K.P., Heiden, V., Rothe, F.**, *Non-homogeneous spatial distributions of populations*, J. Math. Biol. 1, 165-176 (1974).

7. **Hastings, A.**, *Global stability in Lotka-Volterra systems with Diffusion*, J. Math. Biology 6, 163-168 (1978).

8. **Hastings, A.**, *Dynamics of a Single Species in a Spatially Varying Environment: The Stabilizing Role of High Dispersal Rates*, J. Math. Biol. 16, 49-55 (1982).

9. **Levin, S.A.**, *Population model and community structure in heterogeneous environments, in Mathematical Ecology*, T.G.Hallam and S.A.Levin,eds., Springer, New York, 295-321 (1986).

10. **Levin, S.A.**, *Dispersion and population interactions*, Am. Nat. 108, 207-228 (1974).

11. **McMurtrie, R.**, *Persistence and stability of single species and prey predator system in spatially heterogeneous environments*, Mathl. Biosc., 39: 11-51 (1978).

12. **Munn, R.E.** and **Fedorov, V.**, *The Environmental assessment, IIASA Project Report*, vol.1, International Institute for Applied Systems Analysis, Laxenburg, Austria (1986).

13. **Nallaswamy, R.** and **Shukla, J.B.**, *Effects of convective and dispersive migration on the linear stability of a two species system with mutualistic interactions and functional response*, Bul. Math. Biol. 44, 271-282 (1982).

14. **Shigesada, N.** and **Roughgarden, J.**, *The role of rapid dispersal in the population dynamics of competition*, Theor. Pop. Biol. 21, 353 - 372 (1982).

15. **Shukla, J.B.**, **Freedman, H.I.**, **Pal, V.N.**, **Mishra, O.P.**, **Agarwal, M.**, and **Shukla, A.**, *Degradation and subsequent regeneration of a resource : A mathematical model*, Ecol. Modelling, 44, 219-229, (1989).

16. **Shukla, J.B.** and **Verma, S.**, *Effect of convective and dispersive interactions on the stability of two species*, Bul. Math. Biol. 43, 593-610, (1981).

Chapter 4

A Prey-Predator Type Model with Diffusion in Homogeneous and Two-Patch Habitats

4.1 Introduction

An interesting problem in mathematical ecology is to study the growth and co-existence of species with diffusion in both homogeneous and heterogeneous habitats. A diffusion process in the habitat tends to give rise to a uniform density of population in space. As a consequence, it is expected that diffusion, when it occurs, plays the role of increasing stability in a system of interacting populations [1,4 $\rightarrow$ 10, 13 $\rightarrow$ 26,28,29 and their cross references]. Levin [14, 15] has given elaborate survey of models with diffusion in both homogeneous and heterogeneous environment. McMurtrie [16], has also surveyed the literature related to populations model with diffusion and reported the effects of dispersal and spatial heterogeneity on stability of both single species and for Predator-Prey system. Hastings [9], has studied the global stability in n-species Lotka-Volterra systems with diffusion. He also established a necessary and sufficient conditions for stability of a single species model in the

case of large diffusion rates [9]. Nallaswamy and Shukla [18], considered a prey-predator model with functional response and diffusion and have shown, that if the equilibrium state is linearly stable, a subregion of the positive quadrant can be found in the phase plane where it is non-linearly stable with or without diffusion. Freedman and Shukla [4], have studied the effect of a predator resource on a diffusive Predator-Prey system, showing the stabilizing role of diffusion. There is an important exception, known as "diffusive instability" [19, 20, 24, 31, 32], however which might not be a rare event especially in aquatic systems.

In most of the above mentioned studies the existence of the uniform steady state has been assumed and the corresponding model is analyzed in some particular cases. In a few cases the stability of non-uniform steady state has also been studied in a homogeneous environment [33]. It may, however, be noted that in real ecosystems the habitats are often patchy due to resource depletion or environmental changes and populations are usually distributed heterogeneously in their habitats. It may be pointed out that here that little effort has been made to study such systems with diffusion in a patchy habitat using mathematical models. Freedman et al. [5] and Freedman and Wu [6], have studied a single species diffusion model by assuming that the habitat consists of respectively two and three adjoining patches. In [5] Freedman et al. have shown that there exists a positive, monotonic, continuous non-uniform steady state solution that is locally asymptotically stable under both reservoir and no-flux boundary conditions. They, however, did not study the stability of non-linear system, nor the case of two species interaction in a patchy habitat.

In this chapter, we, therefore, study a logistically growing two species prey-predator type model with diffusion in a homogeneous (non-patchy) and two-patch habitats and discuss the stability of both the linear and non-linear systems, under both the reservoir and no-flux boundary conditions. The model is proposed by keeping in view the depletion of forest resources by industrialization and population causing patchiness in the Doon Valley situated at the foot hills of Himalayas in India, [25].

4.2 Mathematical Model

We consider a dynamic model of two logistically growing species with prey-predator type interaction and diffusion in a two-patch forest habitat by assuming that the second species (i.e. predator population) uses the first species (prey population) as an alternative resource. In such a case the rate of change of density of the first species decreases due increase in the density of the second species, but the density of the second species increases due to the increase in the density of the first species in both the patches. Let $x_i(s,t)$ and $y_i(s,t)$ be the densities of first and second species in the i-th patch respectively. Then the model can be written as the following system of autonomous partial differential equations:

$$\frac{\partial x_i(s,t)}{\partial t} = x_i(s,t)\mathrm{g}_i\left(x_i(s,t)\right) - y_i(s,t)\mathbf{p}_i\left(x_i(s,t)\right) + D_{1i}\frac{\partial^2 x_i(s,t)}{\partial s^2} \tag{4.1}$$

$$\frac{\partial y_i(s,t)}{\partial t} = y_i(s,t)\mathrm{f}_i\left(y_i(s,t)\right) + \gamma_i y_i(s,t)\mathbf{p}_i\left(x_i(s,t)\right) + D_{2i}\frac{\partial^2 y_i(s,t)}{\partial s^2} \tag{4.2}$$

$$0 \le s \le L_2, \quad i = 1,2, \quad \gamma_i \ge 0$$

where the i-th patch is assumed to lie along the spatial length $L_{i-1} \le s \le L_i$ $(L_0 = 0)$, $\mathrm{g}_i(x_i)$ and $\mathrm{f}_i(y_i)$ are the respective specific growth rates, $\mathbf{p}_i(x_i)$ is the interaction rates, and D_{1i} and D_{2i} are the diffusion coefficients of x_i and y_i in the two patches, $\gamma_i \ge 0$ be the growth rate coefficient of y_i due to x_i in the i-th patch respectively.

In writing the system (4.1) and (4.2) it is assumed that the growth rates and carrying capacities of two species are smaller or larger in the first patch than their corresponding values in the second patch depending upon whether the first patch is more or less depleted. Thus we assume $\mathrm{g}_i(x_i)$ and $\mathrm{f}_i(y_i)$ are logistic type functions and satisfying $\mathbf{H}_1$:

$\mathbf{H}_1$: $\mathrm{g}_i(x_i),\ \mathrm{f}_i(y_i) \in \mathrm{C}^2[0,\infty)$

$\mathrm{g}_i(0) > 0$, for $x_i > 0$, $\mathrm{g}_i'(x_i) \le 0$,

$\mathrm{f}_i(0) > 0$, for $y_i > 0$, $\mathrm{f}_i'(y_i) \le 0$

$\mathrm{g}_i(K_i) = 0$, $\mathrm{f}_i(M_i) = 0$, $i = 1,2$.

Where K_i, M_i are the carrying capacity of the first and second species respectively in the i-th patch.

In (4.1) the functional response (predator response function) $\mathrm{p}_i(x_i)$ satisfies the following conditions;

H_2 : $\mathrm{p}_i(x_i) \in \mathrm{C}^2[0,\infty)$

$\mathrm{p}_i(0) = 0,$ for $x_i > 0$, $\mathrm{p}_i'(x_i) > 0$, $i = 1, 2$.

Several types of $\mathrm{g}_i(x_i)$, $\mathrm{f}_i(y_i)$ and $\mathrm{p}_i(x_i)$ have been catalogued in [10]. For examples, $\mathrm{g}_i(x_i) = r_i[1-(x_i/K_i)]$, $\mathrm{g}_i(x_i) = r_i(K_i - x_i)/(K_i + \epsilon_i x_i)$ or $\mathrm{g}_i(x_i) = r_i[1-(x_i/K_i)^c]$, $1 \geq c > 0$. Similar forms are also valid for $\mathrm{f}_i(y_i)$. The predator response function, $\mathrm{p}_i(x_i)$ is assumed to be bounded above and examples for which are, $\mathrm{p}_i(x_i) = \alpha_i x_i/(a_i + x_i)$, $\mathrm{p}_i(x_i) = \alpha_i x_i$ or $\mathrm{p}_i(x_i) = \alpha_i(1 - e^{-a_i x_i})$.

We further assume that,

H_3: $\exists\; x_i^* > 0$, $y_i^* > 0$ such that

$$x_i^* \mathrm{g}_i(x_i^*) - y_i^* \mathrm{p}_i(x_i^*) = 0 \tag{4.3}$$

$$y_i^* \left[\mathrm{f}_i(y_i^*) + \gamma_i \mathrm{p}_i(x_i^*)\right] = 0 \tag{4.4}$$

From (4.3) and $\mathbf{H_2}$, we have $\mathrm{g}_i(x_i^*) \geq 0$. From $\mathbf{H_1}$, we note that $\mathrm{g}_i(K_i) = 0$ and $\mathrm{g}_i'(x_i) \leq 0$, $\forall\; x_i \geq 0$. This implies that $\mathrm{g}_i(x_i^*) \geq 0 = \mathrm{g}_i(K_i)$. Hence $x_i^* \leq K_i$. Also from (4.4), $(\mathbf{H_1})$ and $(\mathbf{H_2})$, we get $y_i^* \geq M_i$.

The continuous matching conditions at the interface $s = L_1$ for the system (4.1) and (4.2), are assumed to be

$$x_1(L_1, t) = x_2(L_1, t), \text{ and } y_1(L_1, t) = y_2(L_1, t). \tag{4.5}$$

The continuous flux matching conditions at the interface $s = L_1$ are written as,

$$D_{11}\frac{\partial x_1(L_1,t)}{\partial s} = D_{12}\frac{\partial x_2(L_1,t)}{\partial s} \tag{4.6}$$

$$D_{21}\frac{\partial y_1(L_1,t)}{\partial s} = D_{22}\frac{\partial y_2(L_1,t)}{\partial s} \tag{4.7}$$

The model is studied under two set of boundary conditions i.e. reservoir and no-flux. In the case of reservoir boundary conditions, we take

$$x_1(0,t) = x_1^* \ , \ x_2(L_2,t) = x_2^* \tag{4.8}$$

$$y_1(0,t) = y_1^* \ , \ y_2(L_2,t) = y_2^* \tag{4.9}$$

In the case of no-flux boundary conditions , we have

$$\frac{\partial x_1(0,t)}{\partial s} = 0 = \frac{\partial x_2(L_2,t)}{\partial s} \tag{4.10}$$

$$\frac{\partial y_1(0,t)}{\partial s} = 0 = \frac{\partial y_2(L_2,t)}{\partial s} \tag{4.11}$$

Finally the model is completed by assuming some positive initial distribution, that is, for $i = 1,2$,

$$x_i(s,0) = \chi_i(s) > 0, \ L_{i-1} < s < L_i \tag{4.12}$$

$$y_i(s,0) = \delta_i(s) > 0, \ L_{i-1} < s < L_i \tag{4.13}$$

We first study the existence and stability behavior of the system (4.1) and (4.2) in a homogeneous habitat without patchiness, the effect of patchiness will be investigated later.

4.3 Analysis of the Model in a Homogeneous Habitat

4.3.1 Model without Diffusion

In this case $x_i = x$, $y_i = y$, $\mathrm{g}_i(x_i) = \mathrm{g}(x)$, $\mathrm{f}_i(y_i) = \mathrm{f}(y)$, $\mathrm{p}_i(x_i) = \mathrm{p}(x)$, $i = 1,2$. Thus the system (2.1) and (2.2) reduces to the following form:

$$\frac{dx}{dt} = x\mathrm{g}(x) - y\mathrm{p}(x) \tag{4.14}$$

$$\frac{dy}{dt} = y[\mathbf{f}(y) + \gamma \mathbf{p}(x)] \tag{4.15}$$

This is a Prey-Predator type model, where the density y of predator species, partially depend upon the density x of prey species. In absence of prey, predator grows logistically, i.e. predator has an alternative resource. The functions $\mathbf{g}(x)$, $\mathbf{f}(y)$ and $\mathbf{p}(x)$ satisfy the same type of assumption as mentioned in $\mathbf{H_1}$ and $\mathbf{H_2}$. And the assumption $\mathbf{H_3}$ can be written as, $\exists\ x^* > 0$ and $y^* > 0$ such that,

$$x^*\mathbf{g}(x^*) - y^*\mathbf{p}(x^*) = 0 \tag{4.16}$$

$$y^*[\mathbf{f}(y^*) + \gamma \mathbf{p}(x^*)] = 0 \tag{4.17}$$

From equations (4.16) and (4.17) it follows that there are four equilibria, namely (i) $E_0 = [0,0]$, (ii) $E_K = [K,0]$, (iii) $E_M = [0,M]$ and (iv) $E^* = [x^*, y^*]$. The existence of E^*, the interior equilibrium can be noted from the Fig.4.2. See also [3]. The nature of x^* and y^* with respect to various parameters is shown in the table 4.1, which can be checked analytically.

Table 4.3: Effects of various parameters on x^* and y^*.

(i)	$\mathbf{g}(0)\uparrow$	$x^*\uparrow$	$y^*\uparrow$
(ii)	$\mathbf{f}(0)\uparrow$	$x^*\uparrow$	$y^*\downarrow$
(iii)	$K\uparrow$	$x^*\uparrow$	$y^*\uparrow$
(iv)	$M\uparrow$	$x^*\downarrow$	$y^*\uparrow$
(v)	$\gamma\uparrow$	$x^*\downarrow$	$y^*\uparrow$

In particular it is noted from the table that if the carrying capacity of predator species (i.e. M) increases then x^* decreases and y^* increases. (see also Fig.4.2).

The variational matrix in the general case is given by

$$[M] = \begin{bmatrix} \mathbf{g}(x) + x\mathbf{g}'(x) - y\mathbf{p}'(x) & -\mathbf{p}(x) \\ \gamma y\mathbf{p}'(x) & \mathbf{f}(y) + y\mathbf{f}'(y) + \gamma\mathbf{p}(x) \end{bmatrix}. \tag{4.18}$$

Now calculating the variational matrix from (4.18) for each equilibria and noting the hypotheses $\mathbf{H_1} \rightarrow \mathbf{H_3}$ and the standard stability theory of ordinary differential equations, we note the following obvious remarks:

The equilibrium point E_0 is always unstable. The equilibrium point E_K is a stable or saddle point according as $\mathbf{f}(0)+\gamma\mathbf{p}(K)$ is negative or positive. Similarly the E_M is a stable or saddle point according as $\mathbf{g}(0) - M\mathbf{p}'(0)$ is negative or positive. In general, there is no obvious remark to be made about the stability of the most interesting non-zero equilibria E^*, if it exists.

Therefore, our aim of this section is to obtain local stability and instability as well as global stability conditions for E^*.

We now state main results of this section in Theorem 4.3.1, 4.3.2 and 4.3.3 and Lemma 4.3.1.

Theorem 4.3.1 *The equilibrium E^* is locally asymptotically stable, if $H^* \leq 0$, where*

$$\begin{aligned} H^* &= x^*\mathbf{g}'(x^*) + \mathbf{g}(x^*) - y^*\mathbf{p}'(x^*) \\ &= x^*\mathbf{g}'(x^*) + \mathbf{g}(x^*) - \frac{x^*\mathbf{g}(x^*)}{\mathbf{p}(x^*)}\mathbf{p}'(x^*) \end{aligned} \tag{4.19}$$

Proof: Consider a positive definite function V(x,y) with respect to (x^*,y^*) in the positive quadrant,

$$V(x,y) = \frac{1}{2}\left[\gamma\left(\frac{\mathbf{p}'(x^*)}{\mathbf{p}(x^*)}\right)(x-x^*)^2 + \frac{1}{y^*}(y-y^*)^2\right].$$

We now compute the derivative of V with respect to t along solutions of system (4.14) and (4.15), then expand $\dot{V}$ about (x^*,y^*), we get,

$$\begin{aligned} \dot{V}(x,y) &= \gamma(x-x^*)\left(\frac{\mathrm{p}'(x^*)}{\mathrm{p}(x^*)}\right)\frac{dx}{dt}+\frac{(y-y^*)}{y^*}\frac{dy}{dt} \qquad (4.20)\\ &= \gamma(x-x^*)^2\frac{\mathrm{p}'(x^*)}{\mathrm{p}(x^*)}H^*+(y-y^*)^2\mathrm{f}'(y^*)\\ &+ (x-x^*)(y-y^*)\left[-\gamma\frac{\mathrm{p}'(x^*)}{\mathrm{p}(x^*)}\mathrm{p}(x^*)+\gamma\mathrm{p}'(x^*)\right]+H.O.T.\\ &= \gamma(x-x^*)^2\frac{\mathrm{p}'(x^*)}{\mathrm{p}(x^*)}H^*+(y-y^*)^2\mathrm{f}'(y^*)+H.O.T.* \qquad (4.21)\end{aligned}$$

where $H^* = x^*\mathrm{g}'(x^*) + \mathrm{g}(x^*) - y^*\mathrm{p}'(x^*)$.

Therefore $\dot{V}(x,y)$ is negative definite in the neighborhood of E^* provided $H^* < 0$. Hence the theorem. ∎

The next result shows that E^* will be unstable if H^* is sufficiently positive, in fact we can find an explicit lower bound for H^* by using Chetayev instability theorem.

Theorem 4.3.2 *If*

$$H^* > \frac{\gamma\mathrm{p}(x^*)\mathrm{p}'(x^*)}{-\mathrm{f}'(y^*)} > 0 \qquad (4.22)$$

then E^* is unstable.

Proof: We now use the instability theorem of Chetayev to prove the theorem. Let

$$U(x,y) = \frac{1}{2}\left[(x-x^*)^2 - c_1(y-y^*)^2\right] \qquad (4.23)$$

where $c_1 > 0$. It is noted that $U(x,y) > 0$ in the interior of a cone C, with principal axis parallel to the x-axis and vertex at (x^*,y^*). As before we now compute $\dot{U}(x,y)$ along the solution of the system in the neighbourhood of E^* to get

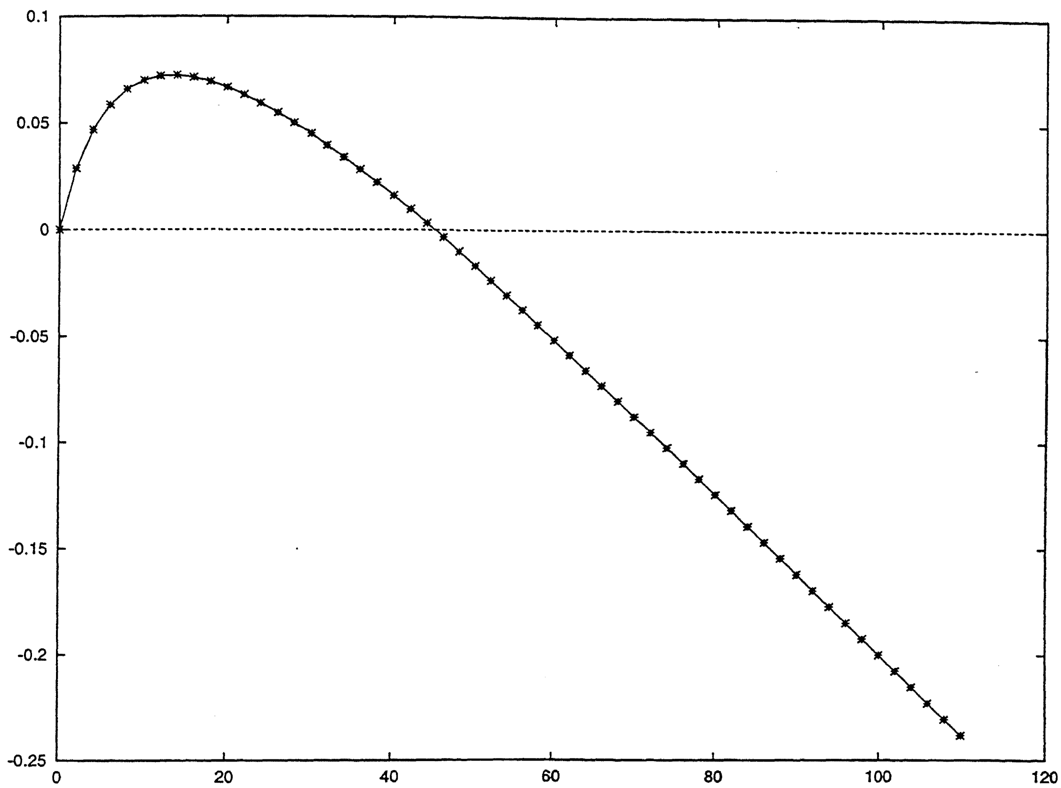


Figure 4.1: The function H^* with respect to x^*.

The final result of this section, Theorem 4.3.3 gives us the criteria for E^* to be globally asymptotically stable. First we prove a lemma which establishes a region of attraction of the system.

Lemma 4.3.1 *The region of attraction for all solutions initiating in the non-negative quadrant is*

$$\mathcal{A} = \{(x, y) : 0 \le x \le K, 0 \le y \le M\frac{[f(0) + \gamma \mathbf{p}_\infty]}{f(0)}\}$$

Proof: From system (4.14) and (4.15), and hypotheses $(\mathbf{H_1})$-$(\mathbf{H_3})$, we get that $\dot{x}(t) \le x(t)\mathrm{g}(x(t)) \le \mathrm{g}(0)x(t)[1 - x(t)/K]$, then $lim\ sup_{t\to\infty}x(t) \le K$, for $x(0) < K$. Similarly we can show that $lim\ sup_{t\to\infty}x(t) \to K$, for $x(0) > K$. We now consider $\dot{y}(t) = y(t)[\mathbf{f}(y(t)) + \gamma\mathbf{p}(x(t))]$. Then, $\dot{y}(t) \le y(t)[\mathbf{f}(0)(1 - y(t)/M) + \mathbf{p}_\infty]$. Hence

$$lim\ sup_{t\to\infty}y(t) \le M[\mathbf{f}(0) + \gamma\mathbf{p}_\infty]/\mathbf{f}(0)$$

We note that solutions initiating on $\partial\mathcal{A} \cap int\ \mathcal{R}^+$ enter into $int\ \mathcal{A}$. Hence $\mathcal{A}$ is an attracting set. ∎

Theorem 4.3.3 *Let the condition*

$$(x - x^*)[x\mathbf{g}(x) - y^*\mathbf{p}(x)] < 0, \quad \forall x \ne x^* \tag{4.27}$$

hold. Then E^* is unique and is globally asymptotically stable in $\mathcal{A}$.

Proof: Let us consider the positive definite function

$$V(s, t) = \gamma \int_{x^*}^{x} \frac{\mathbf{p}(\xi) - \mathbf{p}(x^*)}{\mathbf{p}(\xi)} d\xi + \left(y - y^* - y^* ln\frac{y}{y^*}\right) \tag{4.28}$$

then $\dot{V}(x,y)$, along the solutions of the system, is given by

$$\begin{aligned}
\dot{V}(s,t) &= \gamma\frac{\mathrm{p}(x)-\mathrm{p}(x^*)}{\mathrm{p}(x)}\frac{dx}{dt}+\frac{y-y^*}{y}\frac{dy}{dt} \\
&= \gamma\frac{\mathrm{p}(x)-\mathrm{p}(x^*)}{\mathrm{p}(x)}[x\mathrm{g}(x)-y\mathrm{p}(x)]+(y-y^*)[\mathrm{f}(y)+\gamma\mathrm{p}(x)] \\
&= \gamma\frac{\mathrm{p}(x)-\mathrm{p}(x^*)}{\mathrm{p}(x)}[x\mathrm{g}(x)-y^*\mathrm{p}(x)]-\gamma\frac{\mathrm{p}(x)-\mathrm{p}(x^*)}{\mathrm{p}(x)}[(y-y^*)\mathrm{p}(x)] \\
&+ (y-y^*)[\mathrm{f}(y)+\gamma\mathrm{p}(x^*)]+\gamma(y-y^*)(\mathrm{p}(x)-\mathrm{p}(x^*)) \\
&= \gamma\frac{\mathrm{p}(x)-\mathrm{p}(x^*)}{x-x^*}(x-x^*)\left[\frac{x\mathrm{g}(x)}{\mathrm{p}(x)}-y^*\right]+(y-y^*)^2\left[\frac{\mathrm{f}(y)-\mathrm{f}(y^*)}{y-y^*}\right]
\end{aligned}$$

Now since

$$\frac{\mathrm{p}(x)-\mathrm{p}(x^*)}{x-x^*}>0,\quad \forall x\neq x^* \text{ and } \frac{\mathrm{f}(y)-\mathrm{f}(y^*)}{y-y^*}<0,\quad \forall y\neq y^*.$$

Therefore, $\dot{V}(x,y)$ is negative definite if

$$(x-x^*)\left[\frac{x\mathrm{g}(x)}{\mathrm{p}(x)}-y^*\right]<0,\quad \forall x\neq x^*. \tag{4.29}$$

■

The condition (4.27), implies that as long as the portion of the prey curve $y = x\mathrm{g}(x)/\mathrm{p}(x)$, $0 \le x \le x^*$ lies above the line $y = y^*$ and that the portion of the prey curve $y = x\mathrm{g}(x)/\mathrm{p}(x)$, $x^* \le x \le K$ lies below $y = y^*$, E^* is unique [see Fig.4.2].

Now in the following example we show that the existence of E^* and the condition (4.19) and (4.27) for the local and the global stability are feasible.

Example: Take $\mathrm{g}(x) = r(1 - x/K)$, $\mathrm{f}(y) = s(1 - x/M)$, and $\mathrm{p}(x) = \alpha x$, where $0 < \alpha < 1$. Then the the equilibrium point $E^*(x^*, y^*)$ is given by

$$x^* = \frac{sK(r - \alpha M)}{rs + \alpha^2 \gamma KM}, \quad y^* = \frac{rM(s + \alpha\gamma K)}{rs + \alpha^2\gamma KM}, \quad \text{provided } r > \alpha M.$$

It is also clear from the expression of x^* and y^* that the results shown in the previous table is valid, where $\mathrm{g}(0) = r$, $\mathrm{f}(0) = s$ and rest are same. Further if α increases then x^* decreases and y^* increases, provided $x^* > K/2$.

Now we note that the conditions (4.19) and (4.27) are automatically satisfied, as $H^* = -rx^*/K < 0$ and

$$(x - x^*)[x\mathrm{g}(x) - y^*\mathrm{p}(x)] == -\left[\frac{r}{K}\right] x(x - x^*)^2 < 0, \quad \forall x \neq x^*.$$

Hence E^* is locally as well as globally asymptotically stable.

4.3.2 Model with Diffusion

Now, we wish to consider the model (4.14) and (4.15) with diffusion and analyze the uniform equilibrium E^* under both reservoir and no-flux boundary conditions. The mathematical model in this case can be written as,

$$\frac{\partial x}{\partial t} = x\mathrm{g}(x) - y\mathrm{p}(x) + D_1\frac{\partial^2 x}{\partial s^2} \tag{4.30}$$

$$\frac{\partial y}{\partial t} = y[\mathrm{f}(y) + \gamma\mathrm{p}(x)] + D_2\frac{\partial^2 y}{\partial s^2} \tag{4.31}$$

$$0 \leq s \leq L$$

where $D_i \geq 0$ are diffusion coefficient and $\gamma > 0$ is the conversion of biomass constant. The reservoir and no-flux boundary conditions are respectively,

$$x(0,t) = x^* = x(L,t) \text{ and } y(0,t) = y^* = y(L,t), \tag{4.32}$$

$$\frac{\partial x(0,t)}{\partial s} = 0 = \frac{\partial x(L,t)}{\partial s} \text{ and } \frac{\partial y(0,t)}{\partial s} = 0 = \frac{\partial y(L,t)}{\partial s}. \tag{4.33}$$

Now if we take the following positive definite function

$$W(x,y) = \int_0^L V(x,y)ds,$$

around the equilibrium point E^*, then using similar arguments as in previous section 1. , we get the following theorems for local and global stability of the system.

Theorem 4.3.4 *The equilibrium E^* is locally asymptotically stable, if $H^* \leq 0$, where*

$$H^* = x^*\mathrm{g}'(x^*) + \mathrm{g}(x^*) - y^*\mathrm{p}'(x^*).$$

∎

It is pointed out that even if $H^* > 0$ this uniform equilibrium may become stable with diffusion under a condition as given in the following theorem.

Theorem 4.3.5 *Let $H^* > 0$. Then the equilibrium E^* is locally asymptotically stable, if $H^* \leq D_1\pi^2/L^2$.*

Proof of Theorem 4.3.4 and Theorem 4.3.5 : Consider a positive definite function W(x,y) with respect to (x^*,y^*) in the positive quadrant.

$$W(x,y) = \int_0^L \frac{1}{2}\left[\gamma\left(\frac{\mathrm{p}'(x^*)}{\mathrm{p}(x^*)}\right)(x-x^*)^2 + \frac{1}{y^*}(y-y^*)^2\right] ds \tag{4.34}$$

We now compute the derivative of W with respect to t along solutions of system (4.14) and (4.15), then expand $\dot{V}$ about (x^*,y^*), we get,

$$\begin{aligned} \dot{W}(x,y) &= \int_0^L \left[\gamma(x-x^*)\left(\frac{\mathrm{p}'(x^*)}{\mathrm{p}(x^*)}\right)\frac{\partial x}{\partial t} + \frac{(y-y^*)}{y^*}\frac{\partial y}{\partial t}\right] ds \\ &= \int_0^L C(x-x^*)^2 H^* ds + \int_0^L (y-y^*)^2 \mathrm{f}'(y^*) ds \\ &+ \int_0^L CD_1(x-x^*)\frac{\partial^2 x}{\partial s^2} ds + \int_0^L D_2 \frac{y^*}{y-y^*}\frac{\partial^2 y}{\partial s^2} ds + H.O.T. \end{aligned} \tag{4.35}$$

where $C = \gamma\frac{\mathrm{p}'(x^*)}{\mathrm{p}(x^*)}$ and $H^* = x^*\mathrm{g}'(x^*) + \mathrm{g}(x^*) - y^*\mathrm{p}'(x^*)$. Again

$$\int_0^L CD_1(x-x^*)\frac{\partial^2 x}{\partial s^2}ds = -CD_1\int_0^L\left[\frac{\partial}{\partial s}(x-x^*)\right]^2 ds \quad \text{(Using Integration by Parts)} \tag{4.36}$$

By using Poincare's Inequality, we get

$$-CD_1\int_0^L\left[\frac{\partial(x-x^*)}{\partial s}\right]^2 ds \geq -CD_1\frac{\pi^2}{L^2}\int_0^L(x-x^*)^2 ds \tag{4.37}$$

Therefore $\dot{W}(x,y)$ is negative definite in the neighbourhood of E^* provided $H^* - D_1\pi^2/L^2 < 0$. Hence the theorem 4.3.5. ∎

Theorem 4.3.6 *Let the condition*

$$(x-x^*)[x\mathrm{g}(x) - y^*\mathrm{p}(x)] < 0, \quad \forall x \neq x^*$$

holds. Then E^* is unique and is globally asymptotically stable in $\mathcal{A}$.

Proof: Here we consider the following positive definite function

$$W(x,y) = \int_0^L V(x,y)ds, \tag{4.38}$$

around the solutions space of the above system, where $V(x,y)$ is same as in section 1.4.1.

Differentiating (4.38) with respect to t, we get

$$\begin{aligned}
\dot{W}(s,t) &= \gamma\int_0^L\frac{\mathrm{p}(x)-\mathrm{p}(x^*)}{\mathrm{p}(x)}\frac{\partial x}{\partial t}ds + \int_0^L\frac{y-y^*}{y}\frac{\partial y}{\partial t}ds \\
&= \gamma\int_0^L\frac{\mathrm{p}(x)-\mathrm{p}(x^*)}{x-x^*}(x-x^*)\left[\frac{x\mathrm{g}(x)}{\mathrm{p}(x)} - y^*\right]ds + \int_0^L(y-y^*)^2\left[\frac{\mathrm{f}(y)-\mathrm{f}(y^*)}{y-y^*}\right]ds \\
&+ \gamma D_1\int_0^L\frac{\mathrm{p}(x)-\mathrm{p}(x^*)}{\mathrm{p}(x)}\frac{\partial^2 x}{\partial s^2}ds + D_2\int_0^L\frac{y-y^*}{y}\frac{\partial^2 y}{\partial s^2}ds
\end{aligned} \tag{4.39}$$

Now integrating by parts and using (4.32) or (4.33), we have

$$I_1 = \gamma D_1\int_0^L\frac{\mathrm{p}(x)-\mathrm{p}(x^*)}{\mathrm{p}(x)}\frac{\partial^2 x}{\partial s^2}ds = -\gamma D_1\int_0^L\frac{\mathrm{p}(x^*)}{\mathrm{p}^2(x)}\mathrm{p}'(x)\left(\frac{\partial x}{\partial s}\right)^2 ds < 0$$

and

$$I_2 = D_2 \int_0^L \frac{y - y^*}{y} \frac{\partial^2 y}{\partial s^2} ds = -D_2 \int_0^L \frac{y^*}{y^2} \left(\frac{\partial y}{\partial s}\right)^2 ds < 0.$$

Hence the result. ∎

Thus the uniform equilibrium E^* of the system with diffusion is locally as well as globally asymptotically stable under the same set of conditions, as in the previous case. Further by Theorem 4.3.5, an equilibrium which is unstable without diffusion can become stable with diffusion.

4.4 Analysis of the Model with Diffusion in a Two-Patch Habitat

In the first subsection we study the model (4.1)-(4.13), in the case of uniform steady state. Then in next subsections, we will study the non-uniform state state case.

4.4.1 The Uniform Steady State under Both Sets of Boundary Conditions

The main purpose of this section to show that uniform steady-state in the two patch habitat is globally asymptotically stable. In this case, it is clear that, under both sets of boundary conditions, there is a uniform steady-state, $x_i(s,t) \equiv K^*$, $0 \leq s \leq L_2$, $t \geq 0$, $y_i(s,t) \equiv M^*$, $0 \leq s \leq L_2$, $t \geq 0$, (i=1,2) where K^* and M^* are the common uniform equilibrium of first and second species respectively in the two patches. Here $x_1^* = x_2^* = K^*$ and $y_1^* = y_2^* = M^*$. By using similar arguments and proofs as in section 1.4, the following theorems for stability can be proved for the system (4.1) $\rightarrow$ (4.7) with (4.8) and (4.9) or (4.10) and (4.11).

Theorem 4.4.1 *The equilibrium (K^*, M^*) is locally asymptotically stable, if*

$$H_i^* \leq 0, \quad for \;\; i = 1, 2, \tag{4.40}$$

and the following conditions are satisfied, for $i = 1, 2$

$$[\gamma_i M^* \mathbf{p}_i'(K^*) - \mathbf{p}_i(K^*)]^2 \leq 4H_i^* M^* \mathbf{f}_i'(M^*), \tag{4.41}$$

where

$$H_i^* = K^* \mathbf{g}_i'(K^*) + \mathbf{g}_i(K^*) - M^* \mathbf{p}_i'(K^*) \tag{4.42}$$

Proof: Lineariazing the system (4.1)-(4.2), by using

$$\begin{aligned} x_i(s,t) &= K^* + n_i(s,t) \\ y_i(s,t) &= M^* + m_i(s,t) \end{aligned}$$

we get,

$$\frac{\partial n_i}{\partial t} = n_i[\mathbf{g}_i(K^*) + K^* \mathbf{g}_i'(K^*) - M^* \mathbf{p}_i'(K^*)] - m_i \mathbf{p}_i(K^*) + D_{1i} \frac{\partial^2 n_i}{\partial s^2} \tag{4.43}$$

$$\frac{\partial m_i}{\partial t} = m_i M^* \mathbf{f}_i'(M^*) + n_i \gamma_i M^* \mathbf{p}_i'(K^*) + D_{2i} \frac{\partial^2 m_i}{\partial s^2} \tag{4.44}$$

We considering the following positive definite function,

$$\mathbf{V}(t) = \frac{1}{2} \sum_1^2 \int_{L_{i-1}}^{L_i} \left[(x_i - K^*)^2 + (y_i - M^*)^2 \right] \tag{4.45}$$

where d_i, $i = 1, 2$ are positive constants.

Differentiating (4.45) and using (4.43)-(4.44), we get

$$\begin{aligned} \dot{V} = \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2 H_i^* ds + \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2 M^* \mathbf{f}_i'(M^*) ds \\ + \; & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i [-\mathbf{p}_i(K^*) + \gamma_i M^* \mathbf{p}_i'(K^*)] ds \\ + \; & \sum_1^2 \int_{L_{i-1}}^{L_i} D_{1i} n_i \frac{\partial^2 n_i}{\partial s^2} ds + \sum_1^2 \int_{L_{i-1}}^{L_i} D_{2i} m_i \frac{\partial^2 m_i}{\partial s^2} ds \end{aligned} \tag{4.46}$$

Again using integration by parts, for both type of boundary conditions, we get,

$$\begin{aligned}
\sum_1^2 \int_{L_{i-1}}^{L_i} D_{1i} n_i \frac{\partial^2 n_i}{\partial s^2} ds &= -\sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial n_i}{\partial s}\right)^2 ds \\
\sum_1^2 \int_{L_{i-1}}^{L_i} D_{2i} m_i \frac{\partial^2 m_i}{\partial s^2} ds &= -\sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial m_i}{\partial s}\right)^2 ds.
\end{aligned}$$

Therefore, from (4.46), $\dot{V}$ is negative definite, if the conditions (4.40) and (4.41) are true, for $i = 1, 2$. ∎

Moreover,

Theorem 4.4.2 *Let $H_i^* > 0$. Then the equilibrium (K^*, M^*) is locally asymptotically stable, if the conditions (4.41) along with*

$$H_i^* \le D_{1i} \frac{\pi^2}{(L_i - L_{i-1})^2}, \quad for\, i = 1, 2$$

hold.

Proof: By using Poincare's Inequality, we get

$$D_{1i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial n_i}{\partial s}\right)^2 ds \le D_{1i} \frac{\pi^2}{(L_i - L_{i-1})^2} \int_{L_{i-1}}^{L_i} n_i^2 ds$$

Therefore from (4.46), we get,

$$\begin{aligned}
\dot{V} \le \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2 [H_i^* - D_{1i} \frac{\pi^2}{(L_i - L_{i-1})^2}] ds + \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2 M^* \mathbf{f}_i'(M^*) ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i [-\mathbf{p}_i(K^*) + \gamma_i M^* \mathbf{p}_i'(K^*)] ds - \sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial m_i}{\partial s}\right)^2 ds
\end{aligned}$$

Hence the theorem. ∎

We note here that the stability of uniform equilibrium depends on two respective conditions on H_1^* and H_2^*. Further, the behavior of H_i^*, $i = 1,2$, with respect to K^* is similar to H^* as shown in Fig.4.1. Hence it may be concluded here the patchiness has a destabilising effect if the change in any parameter of the system caused by patchiness due to industrialization, decreases K^*.

We now state the global stability of the uniform steady state.

Theorem 4.4.3 *The uniform steady-state (K^*, M^*) is globally asymptotically stable if*

$$(x_i - K^*)[x_i \mathrm{g}_i(x_i) - M^* \mathrm{p}_i(x_i)] < 0, \quad \forall x_i \neq K^*. \tag{4.47}$$

Proof: Let V(x,y) be the positive definite function about $x = K^*$, $y = M^*$, given by

$$V(x,y) = \sum_1^2 \gamma_i \int_{L_{i-1}}^{L_i} \int_{K^*}^{x_i} \frac{\mathrm{p}_i(\xi_i) - \mathrm{p}_i(K^*)}{\mathrm{p}_i(\xi_i)} d\xi_i ds + \sum_1^2 \int_{L_{i-1}}^{L_i} \left(y_i - M^* - M^* ln \frac{y_i}{M^*} \right) ds \tag{4.48}$$

Differentiating (4.48) with respect to t, and using (4.1) and (4.2) we get,

$$\begin{aligned}
\dot{V}(s,t) &= \sum_1^2 \gamma_i \int_{L_{i-1}}^{L_i} \frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(K^*)}{\mathrm{p}_i(x_i)} \frac{\partial x_i}{\partial t} ds + \sum_1^2 \int_{L_{i-1}}^{L_i} \left(\frac{y_i - M^*}{y_i} \right) \frac{\partial y_i}{\partial t} ds \\
&= \sum_1^2 \gamma_i \int_{L_{i-1}}^{L_i} \frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(K^*)}{x_i - K^*} (x_i - K^*) \left[\frac{x_i \mathrm{g}_i(x_i)}{\mathrm{p}_i(x_i)} - M^* \right] ds \\
&+ \sum_1^2 \int_{L_{i-1}}^{L_i} (y_i - y^*)^2 \left[\frac{\mathrm{f}_i(y_i) - \mathrm{f}_i(M^*)}{y_i - M^*} \right] ds \\
&+ \sum_1^2 \gamma_i D_{1i} \int_{L_{i-1}}^{L_i} \frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(K^*)}{\mathrm{p}_i(x_i)} \frac{\partial^2 x_i}{\partial s^2} ds + \sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} \frac{y_i - M^*}{y_i} \frac{\partial^2 y_i}{\partial s^2} ds
\end{aligned} \tag{4.49}$$

Now consider the integral,

$$\begin{aligned}
I_1 &= \sum_1^2 \gamma_i D_{1i} \int_{L_{i-1}}^{L_i} \frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(K^*)}{\mathrm{p}_i(x_i)} \frac{\partial^2 x_i}{\partial s^2} ds \\
&= \sum_1^2 \gamma_i D_{1i} \left[\frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(K^*)}{\mathrm{p}_i(x_i)} \frac{\partial x_i}{\partial s} \Big|_{L_{i-1}}^{L_i} - \int_{L_{i-1}}^{L_i} \frac{\mathrm{p}_i(K^*) \mathrm{p}_i'(x_i)}{\mathrm{p}_i^2(x_i)} \left(\frac{\partial x_i}{\partial s} \right)^2 ds \right]
\end{aligned}$$

$$
\begin{aligned}
&= -\sum_{1}^{2}\gamma_i D_{1i}\int_{L_{i-1}}^{L_i}\frac{\mathrm{p}_i(K^*)\mathrm{p}_i'(x_i)}{\mathrm{p}_i^2(x_i)}\left(\frac{\partial x_i}{\partial s}\right)^2 ds \\
&+ D_{11}\frac{\partial x_1}{\partial s}(L_1,t)\left[\gamma_1\frac{\mathrm{p}_1(x_1(L_1,t))-\mathrm{p}_1(K^*)}{\mathrm{p}_1(x_1(L_1,t))}-\gamma_2\frac{\mathrm{p}_2(x_1(L_1,t))-\mathrm{p}_2(K^*)}{\mathrm{p}_2(x_1(L_1,t))}\right] \\
&= -\sum_{1}^{2}\gamma_i D_{1i}\int_{L_{i-1}}^{L_i}\frac{\mathrm{p}_i(K^*)\mathrm{p}_i'(x_i)}{\mathrm{p}_i^2(x_i)}\left(\frac{\partial x_i}{\partial s}\right)^2 ds < 0. \qquad (4.50)
\end{aligned}
$$

because under both set of boundary conditions,

$$
[x_1(0,t)-K^*]\frac{\partial x_1}{\partial s}(0,t) = [x_2(L_2,t)-K^*]\frac{\partial x_2}{\partial s}(L_2,t) = 0 \qquad (4.51)
$$

Similarly,

$$
I_2 = \sum_{1}^{2} D_{2i}\int_{L_{i-1}}^{L_i}\frac{y_i-M^*}{y_i}\frac{\partial^2 y_i}{\partial s^2}ds = -\sum_{1}^{2} D_{2i}\int_{L_{i-1}}^{L_i}\left(\frac{\partial y_i}{\partial s}\right)^2 ds < 0 \qquad (4.52)
$$

Hence $\dot V(x,y) < 0$, and $\dot V(K^*,M^*) = 0$. Therefore $\dot V(x,y)$ is negative definite over $x > 0$, $y > 0$ with respect to $x_i^* = K^*$, $y_i^* = M^*$, proving the theorem. ∎

This result generalizes the result of [9, 11] for a patchy habitat.

4.4.2 The Non-Uniform Equilibrium State

Now we consider the model (4.1)-(4.13) and assume the existence of the unsteady state solution of the system [see [22](Theorem 1, page 111 and Theorem 3, page 123)] and also [33]. Our aim here is to show that there exists a positive, monotonic, continuous steady-state solution for the each species separately, with continuous flux at the interface under both reservoir and no-flux boundary conditions and derive the conditions for asymptotic stability of non-uniform equilibrium state.

There are four possible cases:

(1) $x_2^* > x_1^*$ and $y_2^* > y_1^*$
(2) $x_2^* > x_1^*$ and $y_2^* < y_1^*$
(3) $x_2^* < x_1^*$ and $y_2^* < y_1^*$
(4) $x_2^* < x_1^*$ and $y_2^* > y_1^*$

Without loss of generality, (3) can be reduced to (1) and (4) can be reduced to (2). Therefore we study the cases (1) and (2) separately under two set of boundary conditions.

We assume the following conditions on x_i and y_i for $i = 1, 2$.

$$(x_i - x_i^*)[x_i \mathrm{g}_i(x_i) - y_i \mathrm{p}_i(x_i)] < 0, \ \forall x_i \neq x_i^* \text{ and } min.\{y_1^*, y_2^*\} \leq y_i \leq max.\{y_1^*, y_2^*\} \quad (4.53)$$

$$(y_i - y_i^*)[y_i \mathrm{f}_i(y_i) + \gamma_i y_i \mathrm{p}_i(x_i)] < 0, \ \forall y_i \neq y_i^* \text{ and } min.\{x_1^*, x_2^*\} \leq x_i \leq max.\{x_1^*, x_2^*\} \quad (4.54)$$

The analysis in the remaining part of this chapter is valid under these two conditions.

4.4.3 The Model under Reservoir Boundary Conditions: When $x_2^* > x_1^*$ and $y_2^* > y_1^*$.

We first consider the steady-state problem and show that there exists a non-uniform positive monotonic solutions $u_i(s)$, $v_i(s)$ under reservoir boundary conditions and with continuous flux at the interface.

The steady-state system takes the form

$$D_{1i} \frac{d^2 u_i(s)}{ds^2} + u_i \mathrm{g}_i(u_i) - v_i \mathrm{p}_i(u_i) = 0 \quad (4.55)$$

$$D_{2i} \frac{d^2 v_i(s)}{ds^2} + v_i \mathrm{f}_i(v_i) + \gamma_i v_i \mathrm{p}_i(u_i) = 0 \quad (4.56)$$

The reservoir boundary conditions are

$$u_1(0) = x_1^*, u_2(L_2) = x_2^* \quad (4.57)$$

$$v_1(0) = y_1^*, v_2(L_2) = y_2^* \quad (4.58)$$

The continuous solutions and flux matching condition at the interface

$$u_1(L_1) = u_2(L_1); v_1(L_1) = v_2(L_1) \quad (4.59)$$

$$D_{11} \frac{du_1(L_1)}{ds} = D_{12} \frac{du_2(L_1)}{ds} \quad (4.60)$$

$$D_{21}\frac{dv_1(L_1)}{ds} = D_{22}\frac{dv_2(L_1)}{ds} \tag{4.61}$$

Let $p_1(s, \alpha_1)$ and $q_1(s, \beta_1), 0 \leq s \leq L_1$ be the unique solutions of (4.55) and (4.56) respectively, for i=1, such that

$$\frac{\partial p_1(0, \alpha_1)}{\partial s} = \alpha_1, \quad p_1(0, \alpha_1) = x_1^* \tag{4.62}$$

$$\frac{\partial q_1(0, \beta_1)}{\partial s} = \beta_1, \quad q_1(0, \beta_1) = y_1^* \tag{4.63}$$

Let $p_2(s, \alpha_2)$ and $q_2(s, \beta_2), L_1 \leq s \leq L_2$ be the unique solutions of (4.55) and (4.56) respectively, for i=2, such that

$$\frac{\partial p_2(L_2, \alpha_2)}{\partial s} = \alpha_2, \quad p_2(L_2, \alpha_2) = x_2^* \tag{4.64}$$

$$\frac{\partial q_2(L_2, \beta_2)}{\partial s} = \beta_2, \quad q_2(L_2, \beta_2) = y_2^* \tag{4.65}$$

We will have shown the existence of the monotonic solutions if we can show that there exists $\alpha_1, \alpha_2, \beta_1$ and β_2 such that

$$p_1(L_1, \alpha_1) = p_2(L_1, \alpha_2)\ ,\ q_1(L_1, \beta_1) = q_2(L_1, \beta_2) \tag{4.66}$$

$$D_{11}\frac{\partial p_1(L_1, \alpha_1)}{\partial s} = D_{12}\frac{\partial p_2(L_1, \alpha_2)}{\partial s}\ ,\ D_{21}\frac{\partial q_1(L_1, \beta_1)}{\partial s} = D_{12}\frac{\partial q_2(L_1, \beta_2)}{\partial s} \tag{4.67}$$

From (4.55) and (4.56), multiplying both side by $2du_i/ds$ and $2dv_i/ds$ respectively and integrating with respect to s from 0 if i=1 and from L_2 if i=2 , we get,

$$\left[\frac{du_i}{ds}\right]^2 = \alpha_i^2 - \frac{2}{D_{1i}}\int_{x_i^*}^{u_i(s)} [u_i \mathrm{g}_i(u_i) - v_i \mathrm{p}_i(u_i)]du_i(s) \tag{4.68}$$

$$\left[\frac{dv_i}{ds}\right]^2 = \beta_i^2 - \frac{2}{D_{2i}}\int_{y_i^*}^{v_i(s)} [v_i \mathrm{f}_i(v_i) + \gamma_i v_i \mathrm{p}_i(u_i)]dv_i(s) \tag{4.69}$$

Keeping in view of the conditions (4.53) and (4.54), we note here that $p_i(s, \alpha_i)$ and $q_i(s, \beta_i)$ also satisfy the same conditions.

In order to construct our required results we need some preliminary lemmas.

Lemma 4.4.1 *If* $\alpha_1,\ \beta_1 > 0$, *then*

$$\frac{\partial p_1(s,\alpha_1)}{\partial s} > \alpha_1, \quad and \quad \frac{\partial q_1(s,\beta_1)}{\partial s} > \beta_1, \quad on\ 0 < s \le L_1.$$

Proof: From (4.68) , we get,

$$\left[\frac{\partial p_1(s,\alpha_1)}{\partial s}\right]^2 = \alpha_1^2 - \frac{2}{D_{11}}\int_{x_1^*}^{p_1(s,\alpha_1)} [p_1\mathbf{g}_1(p_1) - q_1\mathbf{p}_1(p_1)]dp_1 \tag{4.70}$$

Now using (4.53), it follows from (4.70),

$$\left[\frac{\partial p_1(s,\alpha_1)}{\partial s}\right]^2 \ge \alpha_1^2.$$

Since

$$p_1(0,\alpha_1) = x_1^*, \quad \frac{\partial p_1}{\partial s}(0,\alpha_1) = \alpha_1 \text{ and } p_1(s,\alpha_1) > x_1^*, \text{ for } 0 < s \le L_1.$$

Hence

$$\frac{\partial p_1(s,\alpha_1)}{\partial s} > \alpha_1,\ \forall 0 < s \le L_1.$$

Similarly from (4.69) , we get,

$$\left[\frac{\partial q_1(s,\beta_1)}{\partial s}\right]^2 = \beta_1^2 - \frac{2}{D_{21}}\int_{y_1^*}^{q_1(s,\beta_1)} [q_1\mathbf{f}_1(q_1) + \gamma_1 q_1\mathbf{p}_1(p_1)]dq_1 \tag{4.71}$$

and by using (4.53), we get

$$\frac{\partial q_1(s,\beta_1)}{\partial s} > \beta_1,\ \forall 0 < s \le L_1.$$

Hence the lemma. ∎

Lemma 4.4.2 *If* $\alpha_2,\ \beta_2 > 0,\ 0 < p_2 < x_2^*$ *and* $0 < q_2 < y_2^*$, *then*

$$\frac{\partial p_2(s,\alpha_2)}{\partial s} > \alpha_2, \quad \frac{\partial q_2(s,\beta_2)}{\partial s} > \beta_2, \quad L_1 \le s < L_2.$$

Proof: From (4.68), we have,

$$\left[\frac{\partial p_2(s,\alpha_2)}{\partial s}\right]^2 = \alpha_2^2 - \frac{2}{D_{12}}\int_{x_2^*}^{p_2(s,\alpha_2)} [p_2 g_2(p_2) - q_2 \mathrm{p}_2(p_2)]dp_2 \tag{4.72}$$

Hence by using (4.53) we have, $\partial p_2(s,\alpha_2)/\partial s > \alpha_2$, $L_1 \le s < L_2$ for $0 < p_2 < x_2^*$. Similarly from (4.69) and (4.54), implies $\partial q_2(s,\beta_2)/\partial s > \beta_2$, $L_1 \le s < L_2$ for $0 < q_2 < y_2^*$. ∎

Now we define four continuous maps by the following lemmas, proofs are analogous to lemma 2.3.3 of chapter 2.

Lemma 4.4.3 *Define* $F_{1i}(\alpha_i)$ *by* $F_{1i}(\alpha_i) = p_i(L_1,\alpha_i)$. *Then there exists* $\hat{\alpha}_i > 0$ *such that*

$$F_{11} : [0,\hat{\alpha}_1] \to [x_1^*, x_2^*]$$

$$F_{12} : [0,\hat{\alpha}_2] \to [x_2^*, x_1^*]$$

Lemma 4.4.4 *Define* $F_{2i}(\beta_i)$ *by* $F_{2i}(\beta_i) = q_i(L_1,\beta_i)$. *Then there exists* $\hat{\beta}_i > 0$ *such that*

$$F_{21} : \left[0,\hat{\beta}_1\right] \to [y_1^*, y_2^*]$$

$$F_{22} : \left[0,\hat{\beta}_2\right] \to [y_2^*, y_1^*]$$

In the following theorems we have shown the existence of non-uniform steady state solutions.

Theorem 4.4.4 *There exists a continuous, monotonic solution* u_i *of system (4.55) with continuous flux at* L_1 *(i.e. under (4.66) and (4.67)).*

Proof: From Lemmas 4.4.1 and 4.4.2, it follows that any solution we construct must be monotonically increasing. Again by Lemma 4.4.3, for each $0 \leq \alpha_2 \leq \hat{\alpha}_2$, we can find an α_1 such that $0 \leq \alpha_1 \leq \hat{\alpha}_1$ for which $p_1(L_1, \alpha_1) = p_2(L_1, \alpha_2)$. Hence α_1 can be solved as a function of α_2, $\alpha_1 = h(\alpha_2)$, to give a continuous solution of (4.55) with (4.57), (4.59) and (4.60).

Let

$$\mathrm{G}(\alpha_2) = D_{11}\frac{\partial p_1(L_1, h(\alpha_2))}{\partial s} - D_{12}\frac{\partial p_2(L_1, \alpha_2)}{\partial s}. \tag{4.73}$$

Clearly $\mathrm{G}(\alpha_2)$ is continuous on $0 \leq \alpha_2 \leq \hat{\alpha}_2$. Then we have

$$\mathrm{G}(0) = D_{11}\frac{\partial p_1(L_1, \hat{\alpha}_1)}{\partial s} > 0,$$

and

$$\mathrm{G}(\hat{\alpha}_2) = -D_{12}\frac{\partial p_2(L_1, \hat{\alpha}_2)}{\partial s} < 0.$$

Therefore $\exists\ \bar{\alpha}_2$, $0 < \bar{\alpha}_2 < \hat{\alpha}_2$, such that $\mathrm{G}(\bar{\alpha}_2) = 0$. Hence the theorem. ∎

Exactly similar result is also holds true for the second species,

Theorem 4.4.5 *There exists a continuous, monotonic solution v_i of system (4.56) with continuous flux at L_1 (i.e. under (4.66) and (4.67)).* ∎

We now study the linear and non-linear asymptotic stability of the steady state (4.55) to (4.61) with respect to the system (4.1) $\to$ (4.13).

Theorem 4.4.6 *The steady-state, continuous, monotonic solutions of the linearised system (4.55) and (4.56) with continuous flux at the interface $s = L_1$ is asymptotically stable provided the following conditions are satisfied:*

(i) $\quad \mathcal{G}_{1i}(u_i, v_i) = u_i\mathrm{g}_i'(u_i) + \mathrm{g}_i(u_i) - v_i\mathrm{p}_i'(u_i) \leq 0$,

(ii) $\quad \mathcal{G}_{2i}(u_i, v_i) = v_i\mathrm{f}_i'(v_i) + \mathrm{f}_i(v_i) + \gamma_i\mathrm{p}_i(u_i) \leq 0$, *and*

(iii)
$$[\mathbf{p}_i(u_i) - \gamma_i v_i \mathbf{p}_i'(u_i)]^2 < 4\mathcal{G}_{1i}\mathcal{G}_{2i}$$

for $x_1^* \le u_i \le x_2^*$, $y_1^* \le v_i \le y_2^*$ *and* $i = 1, 2$.

Proof: Let the steady-state solution of system (4.55) be

$$u(s) = \begin{cases} u_1(s), & 0 \le s \le L_1 \\ u_2(s), & L_1 \le s \le L_2 \end{cases}$$

And let the steady-state solution of system (4.56) be

$$v(s) = \begin{cases} v_1(s), & 0 \le s \le L_1 \\ v_2(s), & L_1 \le s \le L_2 \end{cases}$$

Lineariazing (4.1) and (4.2) by using ,

$$x_i(s,t) = u_i(s) + n_i(s,t) \tag{4.74}$$

$$y_i(s,t) = v_i(s) + m_i(s,t) \tag{4.75}$$

We have,

$$\frac{\partial n_i(s,t)}{\partial t} = n_i\left(\mathbf{g}_i(u_i) + u_i\mathbf{g}_i'(u_i)\right) - n_i v_i \mathbf{p}_i'(u_i) - m_i \mathbf{p}_i(u_i) + D_{1i}\frac{\partial^2 n_i}{\partial s^2} \tag{4.76}$$

$$\frac{\partial m_i(s,t)}{\partial t} = m_i\left(\mathbf{f}_i(v_i) + v_i\mathbf{f}_i'(v_i)\right) + m_i\gamma_i \mathbf{p}_i(u_i) + n_i v_i \gamma_i \mathbf{p}_i'(u_i) + D_{2i}\frac{\partial^2 m_i}{\partial s^2} \tag{4.77}$$

Using (4.74) and (4.75) the corresponding initial, boundary and matching conditions can be obtained as follows

$$n_i(s,0) = \chi_i(s) - u_i(s), \; m_i(s,0) = \delta_i(s) - v_i(s)$$

$$n_1(0,t) = 0 = n_2(L_2,t)\;, \; m_1(0,t) = 0 = m_2(L_2,t)$$

$$n_1(L_1,t) = n_2(L_1,t)\;, \; m_1(L_1,t) = m_2(L_1,t)$$
$$D_{11}\frac{\partial n_1}{\partial s}(L_1,t) = D_{12}\frac{\partial n_2}{\partial s}(L_1,t)$$
$$D_{21}\frac{\partial m_1}{\partial s}(L_1,t) = D_{22}\frac{\partial m_2}{\partial s}(L_1,t)$$

Now we consider the following positive definite function,

$$V(t) = \sum_{1}^{2} \int_{L_{i-1}}^{L_i} \frac{1}{2} \left[n_i^2 + m_i^2 \right] ds \tag{4.78}$$

From which we get,

$$\dot{V}(t) = \sum_{1}^{2} \int_{L_{i-1}}^{L_i} \left[n_i \frac{\partial n_i}{\partial t} + m_i \frac{\partial m_i}{\partial t} \right] ds$$

By using (4.76) and (4.77) , we get,

$$\begin{aligned}
\dot{V}(t) &= \sum_{1}^{2} \int_{L_{i-1}}^{L_i} n_i^2 \left[\mathbf{g}_i(u_i) + u_i \mathbf{g}_i'(u_i) \right] ds - \sum_{1}^{2} \int_{L_{i-1}}^{L_i} n_i^2 v_i \mathbf{p}_i'(u_i) ds \\
&- \sum_{1}^{2} \int_{L_{i-1}}^{L_i} n_i m_i \mathbf{p}_i(u_i) ds + \sum_{1}^{2} \int_{L_{i-1}}^{L_i} m_i^2 \left[\mathbf{f}_i(v_i) + v_i \mathbf{f}_i'(v_i) \right] ds \\
&+ \sum_{1}^{2} \gamma_i \int_{L_{i-1}}^{L_i} m_i n_i v_i \mathbf{p}_i'(u_i) ds + \sum_{1}^{2} \gamma_i \int_{L_{i-1}}^{L_i} m_i^2 \mathbf{p}_i(u_i) ds \\
&- \sum_{1}^{2} D_{1i} \int_{L_{i-1}}^{L_i} \left[\frac{\partial n_i}{\partial s} \right]^2 ds - \sum_{1}^{2} D_{2i} \int_{L_{i-1}}^{L_i} \left[\frac{\partial m_i}{\partial s} \right]^2 ds
\end{aligned} \tag{4.79}$$

Therefore $\dot{V}(t)$ is negative definite, if conditions (i), (ii) and (iii) are satisfied. Hence the theorem is proved. ∎

Theorem 4.4.7 *The steady-state, continuous, monotonic solutions of non-linear system (4.55) to (4.61) with continuous flux at the interface $s = L_1$ is asymptotically stable in the subregion of* $\mathbf{R}$: $\{x_1^* \le x_i,\ u_i \le x_2^*,\ y_1^* \le y_i,\ v_i \le y_2^*,$ *for* $i = 1, 2\}$ *provided the following conditions are satisfied:*

(1) $\mathcal{F}_{1i} = \dfrac{x_i \mathbf{g}_i(x_i) - u_i \mathbf{g}_i(u_i) - v_i(\mathbf{p}_i(x_i) - \mathbf{p}_i(u_i))}{x_i - u_i} \le 0$,

(2) $\mathcal{F}_{2i} = \dfrac{y_i[\mathbf{f}_i(y_i) + \gamma_i \mathbf{p}_i(x_i)] - v_i[\mathbf{f}_i(v_i) + \gamma_i \mathbf{p}_i(x_i)]}{y_i - v_i} \le 0$,

(3) $\left[\dfrac{u_i \mathbf{p}_i(x_i)}{x_i} - \gamma_i \dfrac{{v_i}^2}{y_i} \left(\dfrac{\mathbf{p}_i(x_i) - \mathbf{p}_i(u_i)}{x_i - u_i} \right) \right]^2 \le 4 \dfrac{u_i v_i}{x_i y_i} \mathcal{F}_{1i} \mathcal{F}_{2i}$

Proof: From (4.1), (4.2), (4.74) and (4.75), we have

$$\frac{\partial n_i}{\partial t} = (u_i+n_i)\mathrm{g}_i(u_i+n_i) - u_i\mathrm{g}_i(u_i) - (v_i+m_i)\mathrm{p}_i(u_i+n_i) + v_i\mathrm{p}_i(u_i) + D_{1i}\frac{\partial^2 n_i}{\partial s^2} \quad (4.80)$$

$$\frac{\partial m_i}{\partial t} = (v_i+m_i)\mathrm{f}_i(v_i+m_i) - v_i\mathrm{f}_i(v_i) + \gamma_i(v_i+m_i)\mathrm{p}_i(u_i+n_i) - \gamma_i v_i\mathrm{p}_i(u_i) + D_{2i}\frac{\partial^2 m_i}{\partial s^2} \quad (4.81)$$

We now consider the same positive definite function (4.78) as in Theorem 4.4.6. Differentiating (4.78) with respect to t and after using equations (4.80) and (4.81), we get

$$\begin{aligned}
\dot{V}(t) &= \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2 \left[\frac{(u_i+n_i)\mathrm{g}_i(u_i+n_i) - u_i\mathrm{g}_i(u_i)}{n_i}\right] ds \\
&- \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2 \left[v_i\left(\frac{\mathrm{p}_i(u_i+n_i) - \mathrm{p}_i(u_i)}{n_i}\right)\right] ds \\
&- \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i \mathrm{p}_i(u_i+n_i) ds + \sum_1^2 D_{1i}\int_{L_{i-1}}^{L_i} n_i \frac{\partial^2 n_i}{\partial s^2} ds \\
&+ \sum_1^2 c_i \int_{L_{i-1}}^{L_i} m_i^2 \left[\frac{(v_i+m_i)\mathrm{f}_i(v_i+m_i) - v_i\mathrm{f}_i(v_i)}{m_i} + c_i\gamma_i\mathrm{p}_i(u_i+n_i)\right] ds \\
&+ \sum_1^2 \gamma_i \int_{L_{i-1}}^{L_i} m_i n_i \left[v_i\left(\frac{\mathrm{p}_i(u_i+n_i) - \mathrm{p}_i(u_i)}{n_i}\right)\right] ds \\
&+ \sum_1^2 D_{2i}\int_{L_{i-1}}^{L_i} m_i \frac{\partial^2 m_i}{\partial s^2} ds
\end{aligned} \quad (4.82)$$

Now,

$$\frac{\mathrm{p}_i(u_i+n_i) - \mathrm{p}_i(u_i)}{n_i} \geq 0, \quad \text{for all values of } n_i. \quad (4.83)$$

Also by using boundary, matching conditions and $\partial u_i/\partial s > 0$, we have

$$\sum_1^2 D_{1i}\int_{L_{i-1}}^{L_i} n_i \frac{\partial^2 n_i}{\partial s^2} ds = -\sum_1^2 D_{1i}\int_{L_{i-1}}^{L_i} \left(\frac{\partial n_i}{\partial s}\right)^2 ds < 0. \quad (4.84)$$

Similarly

$$\sum_1^2 D_{2i}\int_{L_{i-1}}^{L_i} n_i \frac{\partial^2 m_i}{\partial s^2} ds - \sum_1^2 D_{2i}\int_{L_{i-1}}^{L_i} \left(\frac{\partial m_i}{\partial s}\right)^2 ds < 0. \quad (4.85)$$

Therefore $\dot{V}(t) \leq 0$ if the conditions (1),(2),(3) holds true. Hence the theorem is proved.

∎

It is noted that if we linearize the conditions of theorem 4.4.7, we get the conditions of theorem 4.4.6.

Remark: When $D_{1i} \to 0$, for $i = 1, 2$. In such a case, from (4.55), we have, $v_i = u_i \mathrm{g}_i(u_i)/\mathrm{p}_i(u_i)$. Then the stability condition (i) of theorem 4.4.6 modified as follows,

$$\mathcal{G}_i(u_i) = u_i \mathrm{g}_i'(u_i) + \mathrm{g}_i(u_i) - \frac{u_i \mathrm{g}_i(u_i)}{\mathrm{p}_i(u_i)} \mathrm{p}_i'(u_i).$$

We note that for fixed s, the behavior of the function $\mathcal{G}_i(u_i)$ with respect to u_i is same as that of $H^*(x^*)$ relative to x^*. Hence $\mathcal{G}_i(u_i)$ also becomes less negative if u_i decreases [see Fig.4.1]. In particular if K_1 decreases then x_1^* decreases, therefore for a fixed s, u_1 decrease and $\mathcal{G}_1(u_1)$ becomes less negative. Thus, the effects of those parameters such as K_i, M_i, which decrease u_i, are destabilizing. This implies that if carrying capacity of the prey resource in a particular patch decreases due to depletion of that patch then it is destabilizing.

4.4.4 The Model under Reservoir Boundary Conditions: When $x_2^* > x_1^*$ and $y_1^* > y_2^*$

It can be checked that for $x_2^* > x_1^*$ the monotonicity of steady state solution is similar as the above case and for $y_1^* > y_2^*$, the monotonicity is just the reverse of the above case. [see also Fig.4.5].

In this case also the linear and non-linear asymptotic stability conditions for the steady state system under reservoir boundary conditions are similar as in Theorem 4.4.6 and Theorem 4.4.7.

The above theorems imply that the system will settle down to the steady state distribution in the two patches under certain conditions, the magnitude of the steady state distribution of the prey density being lower than it's original value but the density distribu-

tion of the predator species being correspondingly higher. The above analysis also suggest that patchiness causes destabilization of the system.

4.4.5 The Model under No-flux Boundary Conditions: When $x_2^* > x_1^*$ and $y_2^* > y_1^*$

The steady state system becomes,

$$D_{1i}\frac{d^2u_i(s)}{ds^2} + u_i\mathrm{g}_i(u_i) - v_i\mathrm{p}_i(u_i) = 0 \tag{4.86}$$

$$D_{2i}\frac{d^2v_i(s)}{ds^2} + v_i\mathrm{f}_i(v_i) + \gamma_i v_i\mathrm{p}_i(u_i) = 0 \tag{4.87}$$

The no-flux boundary conditions are,

$$\frac{du_1(0)}{ds} = 0 = \frac{du_2(L_2)}{ds} \tag{4.88}$$

$$\frac{dv_1(0)}{ds} = 0 = \frac{dv_2(L_2)}{ds} \tag{4.89}$$

The continuous and the matching conditions at the interface are,

$$u_1(L_1) = u_2(L_1),\ v_1(L_1) = v_2(L_1) \tag{4.90}$$

$$D_{11}u_1'(L_1) = D_{12}u_2'(L_1),\ D_{21}v_1'(L_1) = D_{22}v_2'(L_1). \tag{4.91}$$

Let $p_1(s,\alpha_1)$ and $q_1(s,\beta_1)$, $0 \le s \le L_1$ are the unique solutions of (4.86) and (4.87) respectively, for i = 1, such that

$$\frac{\partial p_1(0,\alpha_1)}{\partial s} = 0\ ,\ \ p_1(0,\alpha_1) = \alpha_1 \tag{4.92}$$

$$\frac{\partial q_1(0,\beta_1)}{\partial s} = 0\ ,\ \ q_1(0,\beta_1) = \beta_1 \tag{4.93}$$

Let $p_2(s,\alpha_2)$ and $q_2(s,\beta)$, $L_1 \le s \le L_2$ are the unique solutions of (4.86) and (4.87) respectively, for i = 2, such that

$$\frac{\partial p_2(L_2,\alpha_2)}{\partial s} = 0\ ,\ \ p_2(L_2,\alpha_2) = \alpha_2 \tag{4.94}$$

$$\frac{\partial q_2(L_2,\beta_2)}{\partial s} = 0 \ , \ q_1(L_2,\beta_2) = \beta_2 \tag{4.95}$$

We will have shown the existence of the monotonic solutions if we can show that there exists α_1, α_2, β_1 and β_2 such that

$$p_1(L_1,\alpha_1) = p_2(L_1,\alpha_2) \ , \ q_1(L_1,\beta_1) = q_2(L_1,\beta_2) \tag{4.96}$$

$$D_{11}\frac{\partial p_1(L_1,\alpha_1)}{\partial s} = D_{12}\frac{\partial p_2(L_1,\alpha_2)}{\partial s}, \quad D_{21}\frac{\partial q_1(L_1,\beta_1)}{\partial s} = D_{12}\frac{\partial q_2(L_1,\beta_2)}{\partial s} \tag{4.97}$$

From (4.86), multiplying both side by $2du_i/ds$ and integrating w.r.to s from 0 if i=1 and from L_2 if i=2 , we get

$$\left[\frac{du_i}{ds}\right]^2 = -\frac{2}{D_{1i}}\int_{\alpha_i}^{u_i(s)}[u_i\mathrm{g}_i(u_i) - v_i\mathrm{p}_i(u_i)]du_i(s). \tag{4.98}$$

Similarly from (4.87), we have

$$\left[\frac{dv_i}{ds}\right]^2 = -\frac{2}{D_{2i}}\int_{\beta_i}^{u_i(s)}[v_i\mathrm{f}_i(v_i) + \gamma_i v_i\mathrm{p}_i(u_i)]du_i(s). \tag{4.99}$$

Here also we need similar type of lemmas as in the case of reservoir boundary conditions.

Lemma 4.4.5 *If $\alpha_1 > x_1^*$, $\beta_1 > y_1^*$, $p_1 > x_1^*$ and $q_1 > y_1^*$, then*

$$\frac{\partial p_1(s,\alpha_1)}{\partial s} > 0 \ , \ \frac{\partial q_1(s,\beta_1)}{\partial s} > 0 \ , \ 0 < s \leq L_1$$

Proof: From (4.98), we get,

$$\left[\frac{\partial p_1(s,\alpha_1)}{\partial s}\right]^2 = -\frac{2}{D_{11}}\int_{\alpha_1}^{p_1(s,\alpha_1)}[p_1\mathrm{g}_1(p_1) - q_1\mathrm{p}_1(p_1)]\,dp_1 \tag{4.100}$$

Since $\partial p_1(0,\alpha_1)/\partial s = 0$, $p_1(0,\alpha_1) = \alpha_1$ there exists $s_1 > 0$ such that $p_1(s,\alpha_1) > \alpha_1$ on $0 < s < s_1$. If not, let s_0, $0 < s_0 \leq L_1$, be the first positive value , if it exists, such that

$p_1(s_0, \alpha_1) = \alpha_1$. Then by the mean value theorem there exists $\bar{s}$ such that $0 < \bar{s} < s_0$ and $\partial p_1(\bar{s}, \alpha_1)/\partial s = 0$; that is,

$$0 = -\frac{2}{D_{11}} \int_{\alpha_1}^{p_1(\bar{s},\alpha_1)} [p_1 \mathrm{g}_1(p_1) - q_1 \mathrm{p}_1(p_1)]\, dp_1 \tag{4.101}$$

But the right-hand side of (4.101) is nonzero, since $p_1 > \alpha_1$ on $0 < s \leq \bar{s}$. Also $\alpha_1 > x_1^*$, therefore, $p_1 > x_1^*$ and since $q_1 > y_1^*$. This implies that, $p_1 \mathrm{g}_1(p_1) - q_1 \mathrm{p}_1(p_1) < 0$, giving a contradiction. Hence $p_1(s, \alpha_1) > \alpha_1$, for all value $0 < s \leq L_1$. This implies, $p(s, \alpha_1) > x_1^*$, on $0 < s \leq L_1$. Hence by (4.47) and (4.100), the first part of the lemma. Similarly, other part of the lemma follows. ∎

Lemma 4.4.6 *If $0 < p_2(s, \alpha_2) \leq x_2^*$ and $0 < q_2(s, \beta_2) \leq y_2^*$, then $\alpha_2 < x_2^*$ implies $p_2(s, \alpha_2) < \alpha_2$ and $\beta_2 < y_2^*$ implies $q_2(s, \beta_2) < \beta_2$, for $L_1 \leq s < L_2$.*

Proof: Since $0 < p_2(s, \alpha_2) \leq x_2^*$, then from (4.53), we get, $p_2 \mathrm{g}_2(p_2) - y_2^* \mathrm{p}_2(p_2) > 0$. Now Since $0 < q_2(s, \beta_2) \leq y_2^*$ and $\alpha_2 < x_2^*$, then $p_2 \mathrm{g}_2(p_2) - q_2 \mathrm{p}_2(p_2) > 0$, for all α_2, p_2. Hence, from (4.98), $p_2 < \alpha_2$. Again by using (4.99) the follows other part of the lemma. ∎

As in the case of reservoir boundary conditions, ∃ four continuous mapping as follows:

Lemma 4.4.7 *Define $G_{1i}(\alpha_i)$ by $G_{1i}(\alpha_i) = p_i(L_1, \alpha_i)$. Then ∃ $\hat{\alpha}_i$ such that*

$$\begin{aligned} \mathrm{G}_{11} &: [x_1^*, \hat{\alpha}_1] \to [x_1^*, x_2^*], \\ \mathrm{G}_{12} &: [\hat{\alpha}_2, x_2^*] \to [x_1^*, x_2^*]. \end{aligned}$$

∎

Lemma 4.4.8 *Define $G_{2i}(\beta_i)$ by $G_{2i}(\beta_i) = q_i(L_1, \beta_i)$. Then ∃ $\hat{\beta}_i$ such that*

$$\begin{aligned} \mathrm{G}_{21} &: \left[y_1^*, \hat{\beta}_1\right] \to [y_1^*, y_2^*], \\ \mathrm{G}_{22} &: \left[\hat{\beta}_2, y_2^*\right] \to [y_1^*, y_2^*]. \end{aligned}$$

Proof: Same as lemma 2.3.6, (chapter 2). ∎

The existence theorems are given as follows:

Theorem 4.4.8 *(i) There exists a continuous, monotonic solution of system (4.86) with continuous flux at L_1.*

(ii) There exists a continuous, monotonic solution of system (4.87) with continuous flux at L_1.

Proof: Analogous to theorem 1.5.8 and theorem 1.5.9. ∎

Now we state the stability conditions of the system with no-flux boundary condition. Proves are similar to the proofs of theorem 1.5.10 and theorem 1.5.11 . These conditions are the same as in the case of reservoir boundary conditions.

Theorem 4.4.9 *The steady-state, continuous, monotonic solutions of system (4.86) and (4.87) with continuous flux at the interface $s = L_1$ is asymptotically stable provided the following conditions are satisfied:*

(i) $\mathcal{G}_{1i}(u_i, v_i) = u_i\mathbf{g}_i'(u_i) + \mathbf{g}_i(u_i) - v_i\mathbf{p}_i'(u_i) \leq 0$,

(ii) $\mathcal{G}_{2i}(u_i, v_i) = v_i\mathbf{f}_i'(v_i) + \mathbf{f}_i(v_i) + \gamma_i\mathbf{p}_i(u_i) \leq 0,$ *and*

(iii) $$[\mathbf{p}_i(u_i) - \gamma_i v_i \mathbf{p}_i'(u_i)]^2 < 4\mathcal{G}_{1i}\mathcal{G}_{2i}$$

for $x_1^* \leq u_i \leq x_2^*, \quad y_1^* \leq v_i \leq y_2^*$ *and* $i = 1, 2.$

Theorem 4.4.10 *The steady-state, continuous, monotonic solutions of non-linear system (4.86) to (4.91) with continuous flux at the interface $s = L_1$ is asymptotically stable in the subregion of* $\mathbf{R}$:

$$\{x_1^* \leq x_i, \ u_i \leq x_2^*, \ y_1^* \leq y_i, \ v_i \leq y_2^*, \ \textit{for } i = 1, 2\}$$

provided the following conditions are satisfied:

(1) $\mathcal{F}_{1i} = \dfrac{x_i \mathrm{g}_i(x_i) - u_i \mathrm{g}_i(u_i) - v_i(\mathrm{p}_i(x_i) - \mathrm{p}_i(u_i))}{x_i - u_i} \leq 0$,

(2) $\mathcal{F}_{2i} = \dfrac{y_i[\mathrm{f}_i(y_i) + \gamma_i \mathrm{p}_i(x_i)] - v_i[\mathrm{f}_i(v_i) + \gamma_i \mathrm{p}_i(x_i)]}{y_i - v_i} \leq 0$,

(3) $\left[\dfrac{u_i \mathrm{p}_i(x_i)}{x_i} - \gamma_i \dfrac{{v_i}^2}{y_i}\left(\dfrac{\mathrm{p}_i(x_i) - \mathrm{p}_i(u_i)}{x_i - u_i}\right)\right]^2 \leq 4\dfrac{u_i v_i}{x_i y_i}\mathcal{F}_{1i}\mathcal{F}_{2i}$

In this also the similar results for the steady state distributions are valid as in the case of reservoir boundary conditions.

4.4.6 Both the Species have Uniform Equilibrium State in the Second Patch

In this case, the steady-state solutions of both the species are variable in the first patch and constant in second patch, i.e. $u_2 = x_2^*$ and $v_2 = y_2$, $L_1 \leq s \leq L_2$, $t \geq 0$. As shown in the general case we note that here also the steady state solution is positive, continuous and monotonic in the first patch [see Fig.4.8]. For stability analysis we use the positive definite function,

$$V(t) = \frac{1}{2}\left[\int_0^{L_1}(x_1 - u_1)^2 ds + \int_{L_1}^{L_2}(x_2 - x_2^*)^2 ds + \int_0^{L_1}(y_1 - v_1)^2 ds + \int_{L_1}^{L_2}(y_2 - y_2^*)^2 ds\right]$$

and analyze in the similar manner as in Theorem 4.4.6, and can prove the following theorem,

Theorem 4.4.11 *Let $u_2 = x_2^*$ and $v_2 = y_2^*$. Then the steady-state, continuous, monotonic solutions of non-linear system (2.1) to (2.4) and with either (2.5) or (2.6)and with continuous flux at the interface $s = L_1$ is asymptotically stable in the subregion of* $\mathbf{R}$:

$$\{x_1^* \leq x_1,\ u_1 \leq x_2^*,\ y_1^* \leq y_1,\ v_1 \leq y_2^*\}$$

provided the following conditions are satisfied:

(i.a) $$\mathcal{G}_1(u_1, v_1) = u_1\mathrm{g}_1'(u_1) + \mathrm{g}_1(u_1) - v_1\mathrm{p}_1'(u_1) \leq 0\ ,$$

(i.b) $$H_2^* = x_2^*\mathrm{g}_2'(x_2^*) + \mathrm{g}_2(x_2^*) - y_2^*\mathrm{p}_2'(x_2^*) \leq 0,$$

(ii) $$\mathcal{F}_1(u_1, v_1) = v_1\mathrm{f}_1'(v_1) + \mathrm{f}_1(v_1) + \gamma_1\mathrm{p}_1(u_1) \leq 0,$$

(iii.a) $$[\mathrm{p}_1(u_1) - \gamma_1 v_1\mathrm{p}_1'(u_1)]^2 < 4\mathcal{G}_1\mathcal{F}_1$$

(iii.b) $$[\mathrm{p}_2(x_2^*) - \gamma_2 y_2^*\mathrm{p}_2'(x_2^*)]^2 < 4H_2^* y_2^*\mathrm{f}_2'(y_2^*)$$

It is noted here that these condition are less in number then the conditions of the theorem 4.4.6 and more than theorem 4.4.3. Thus the distributions in this case are more stable than the general case but less stable then the uniform distribution in the two patches.

4.5 Numerical Examples

In the following the steady state solutions of couple-reaction diffusion system in a two-patch habitat with reservoir boundary condition and flux matching condition at the interface are obtained numerically to show there existence. For this we consider the following particular form of functions:

$$\mathrm{g}_i(u_i) = r_{1i}(1 - u_i/K_i),\quad \mathrm{f}_i(v_i) = r_{2i}(1 - v_i/M_i),\quad \mathrm{p}_i(u_i) = \frac{\alpha_i u_i}{a_i + b_i u_i},\quad i = 1, 2.$$

Then the steady-state system (4.55) and (4.56), i=1,2, can be modified as follows :

$$D_{1i}\frac{d^2u_i}{ds^2} = r_{1i}u_i(1 - u_i/K_i) - v_i\frac{\alpha_i u_i}{a_i + b_i u_i} \tag{4.102}$$

$$D_{2i}\frac{d^2v_i}{ds^2} = r_{2i}v_i(1 - v_i/M_i) + \gamma_i v_i \frac{\alpha_i u_i}{a_i + b_i u_i} \tag{4.103}$$

The reservoir boundary conditions are:

$$u_1(0) = x_1^*, \quad u_2(L_2) = x_2^*, \quad v_1(0) = y_1^*, \quad v_2(L_2) = y_2^* \tag{4.104}$$

The continuous flux matching conditions at the interface are

$$D_{11}\frac{du_1(L_1)}{ds} = D_{12}\frac{du_2(L_1)}{ds}, \; D_{21}\frac{dv_1(L_1)}{ds} = D_{22}\frac{dv_2(L_1)}{ds} \tag{4.105}$$

$$u_1(L_1) = u_2(L_1), \quad v_1(L_1) = v_2(L_1) \tag{4.106}$$

We solve system of equations (4.102) to (4.106) numerically by using finite difference method in various cases using different set of values for parameters satisfing the stability criteria. The corresponding graphs are shown in Figures 4.3, 4.4, 4.5, 4.6 and 4.7.

From the graphs it can be noted that in all cases the steady state solution is monotonic. In particular from Fig.4.3-4.6, we observe that for all possible combination of x_i^*'s and y_i^*'s, the steady state solutions are always monotonic. In Fig.4.7, the effect of diffusion coefficients on the non-uniform steady state distributions is shown. It is noted from this figure that as respective diffusion coefficients in the two patches increase the steady state solutions tends towards linear distributions. In Fig.4.8, it is shown that if the steady state solutions of both the species have uniform equilibrium state in the second patch, then the steady state distribution is monotonic in the first patch for both the species.

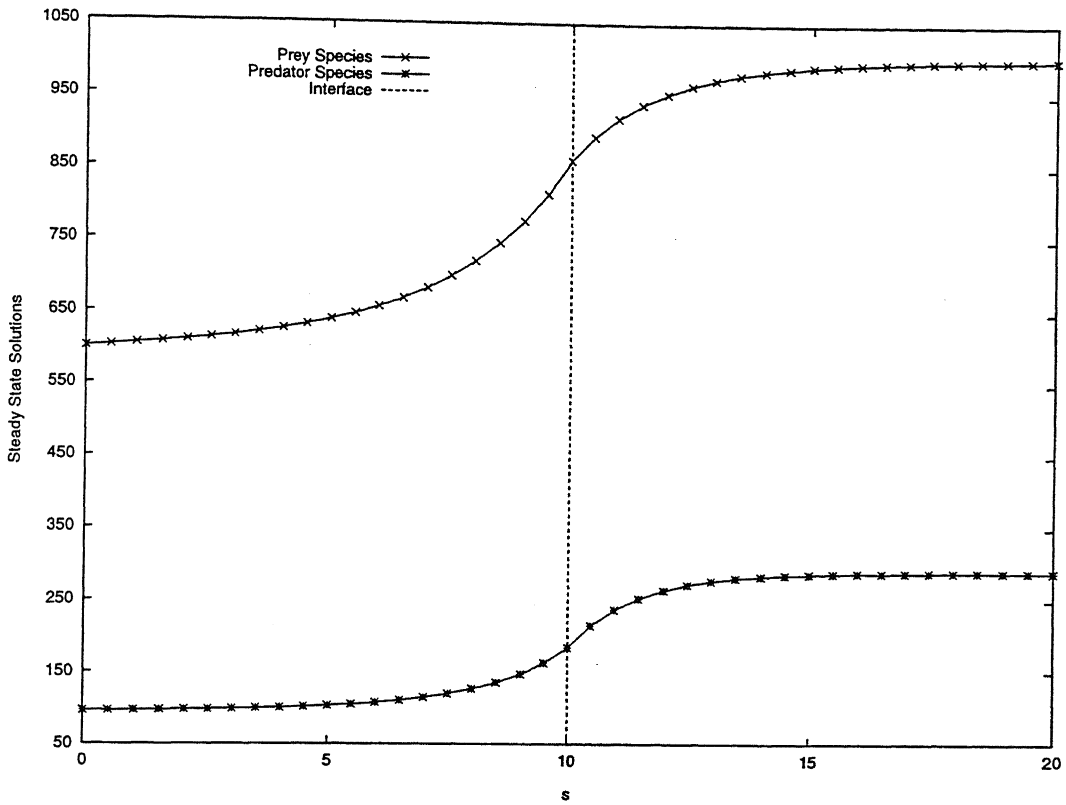


Figure 4.3: The steady state solutions, when $x_1^* = 600 < x_2^* = 1000$, $y_1^* = 100 < y_2^* = 300$.

$r_1 = 0.122$, $K_1 = 610$, $\alpha_1 = 2.000E-05$, $b_1 = 1.000E-06$
$r_2 = 0.418$, $K_2 = 1045$, $\alpha_2 = 6.000E-05$, $b_2 = 1.000E-06$
$s_1 = 0.288$, $M_1 = 96$, $\gamma_1 = 1.000$, $a_1 = 1.0$
$s_2 = 0.418$, $M_2 = 290$, $\gamma_2 = 0.3333$, $a_2 = 1.0$
$D_{11} = 0.5$, $D_{12} = 0.9$, $D_{21} = 0.5$, $D_{22} = 0.9$.

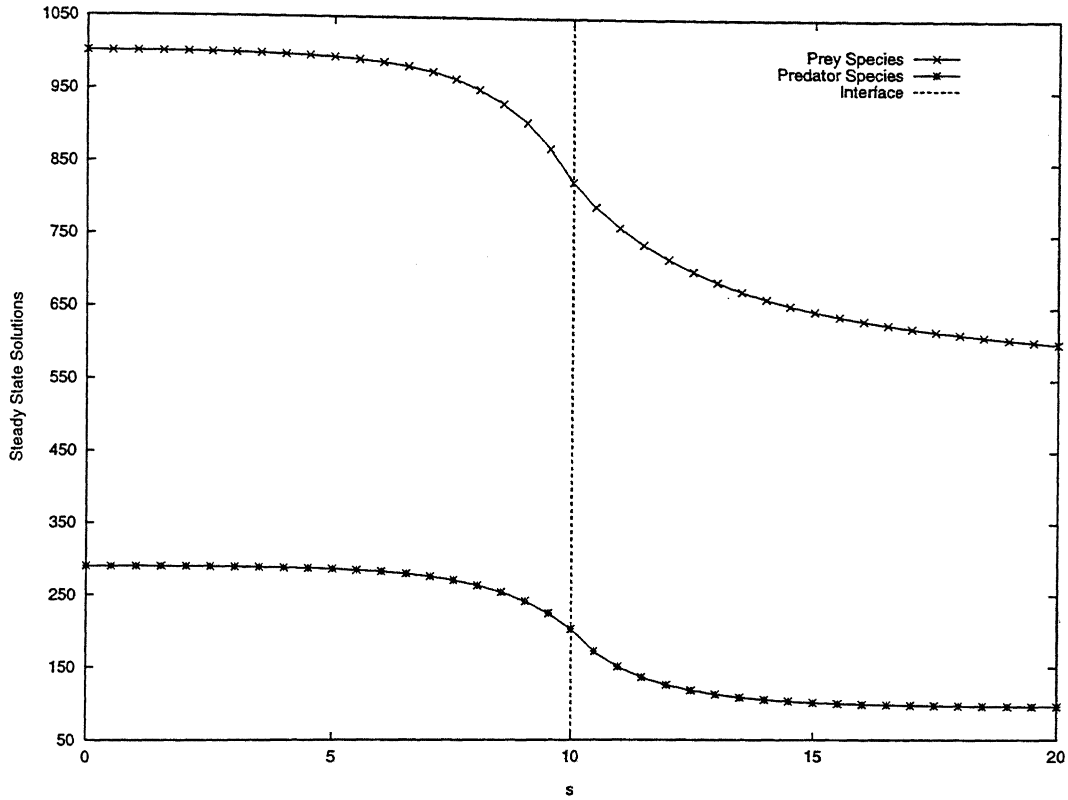


Figure 4.4: The steady state solutions, when $x_1^* = 100 > x_2^* = 60$, $y_1^* = 80 > y_2^* = 50$.

$r_1 = 0.448$, $K_1 = 112$, $\alpha_1 = 6.000E-04$, $b_1 = 1.000E-06$
$r_2 = 0.13$, $K_2 = 65$, $\alpha_2 = 2.000E-04$, $b_2 = 1.000E-06$
$s_1 = 0.14$, $M_1 = 70$, $\gamma_1 = 0.3333$, $a_1 = 1.0$
$s_2 = 0.138$, $M_2 = 46$, $\gamma_2 = 1.0000$, $a_2 = 1.0$
$D_{11} = 0.9$, $D_{12} = 0.6$, $D_{21} = 0.5$, $D_{22} = 0.7$.

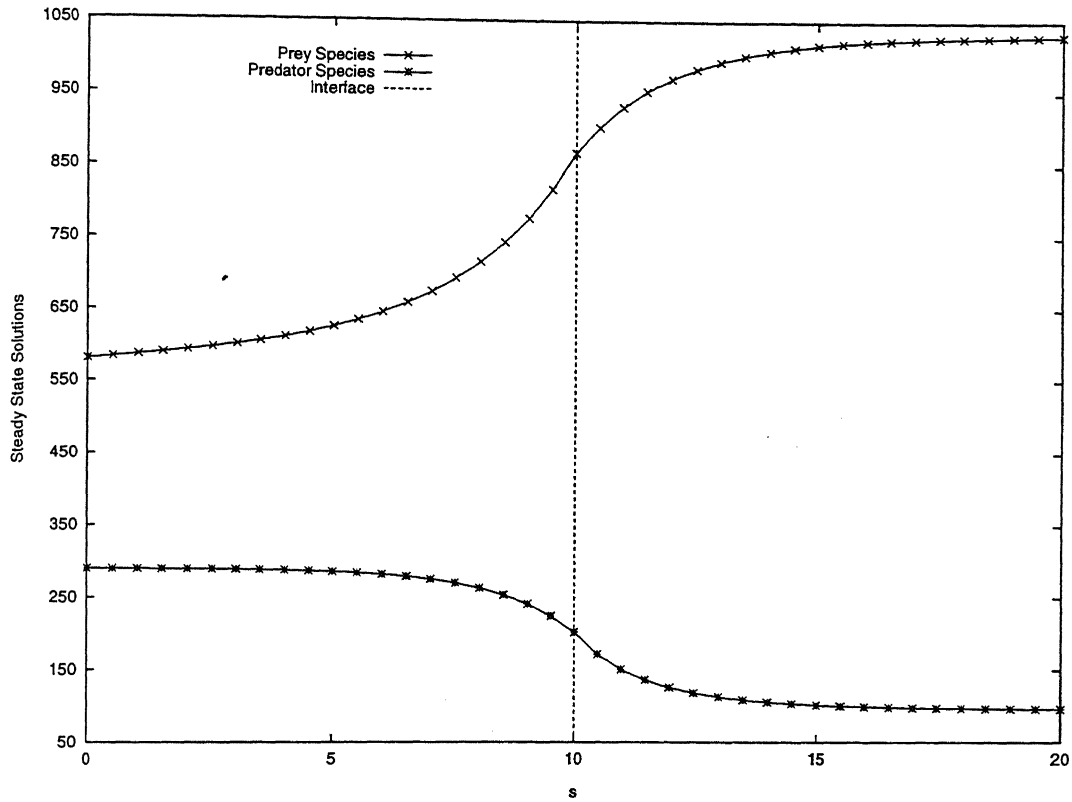


Figure 4.5: The steady state solutions, when $x_1^* = 50 < x_2^* = 100$, $y_1^* = 80 > y_2^* = 40$.

$r_1 = 0.174$, $K_1 = 58$, $\alpha_1 = 3.000E - 04$, $b_1 = 1.000E - 06$

$r_2 = 0.312$, $K_2 = 104$, $\alpha_2 = 3.000E - 04$, $b_2 = 1.000E - 06$

$s_1 = 0.316$, $M_1 = 79$, $\gamma_1 = 0.26666$, $a_1 = 1.0$

$s_2 = 0.152$, $M_2 = 38$, $\gamma_2 = 0.26666$, $a_2 = 1.0$

$D_{11} = 0.4$, $D_{12} = 0.4$, $D_{21} = 0.4$, $D_{22} = 0.4$.

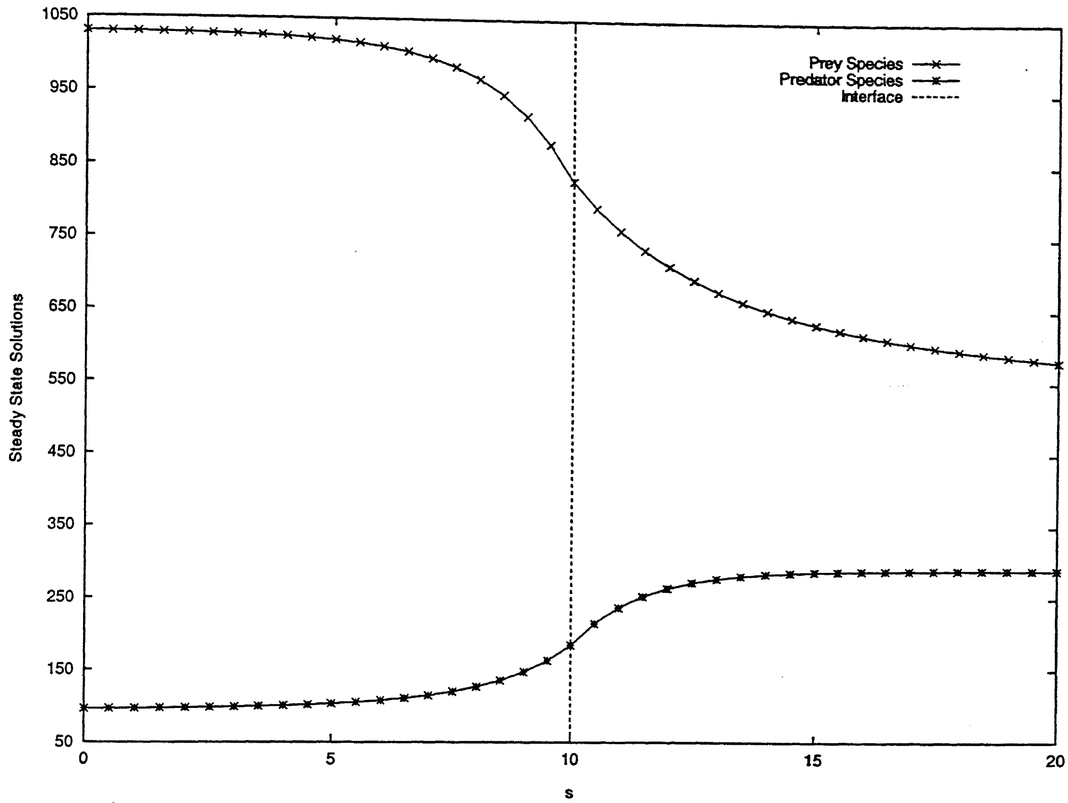


Figure 4.6: The steady state solutions, when $x_1^* = 100 > x_2^* = 40$, $y_1^* = 50 < y_2^* = 80$.

$r_1 = 0.23$,	$K_1 = 115$,	$\alpha_1 = 6.000E-04$,	$b_1 = 1.00E-06$
$r_2 = 0.128$,	$K_2 = 64$,	$\alpha_2 = 6.000E-04$,	$b_2 = 1.00E-06$
$s_1 = 0.08$,	$M_1 = 40$,	$\gamma_1 = 0.3333$,	$a_1 = 1.0$
$s_2 = 0.152$,	$M_2 = 76$,	$\gamma_2 = 0.3333$,	$a_2 = 1.0$
$D_{11} = 0.4$,	$D_{12} = 0.5$,	$D_{21} = 0.4$,	$D_{22} = 0.7$.

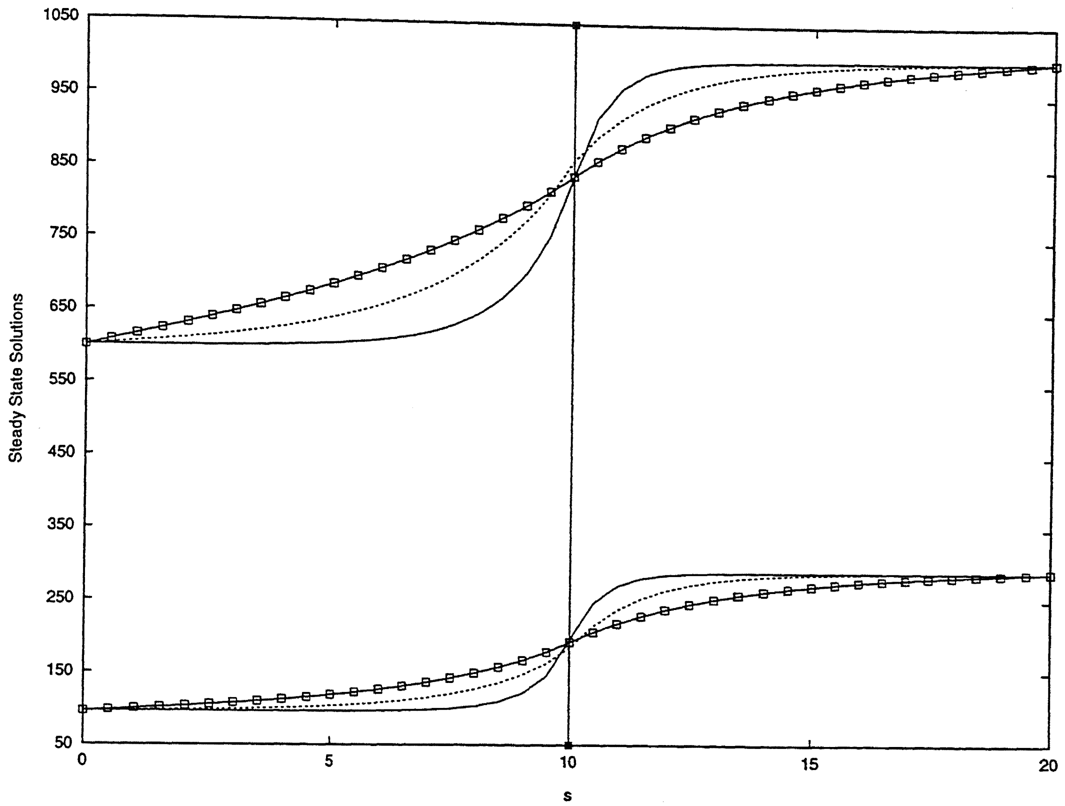
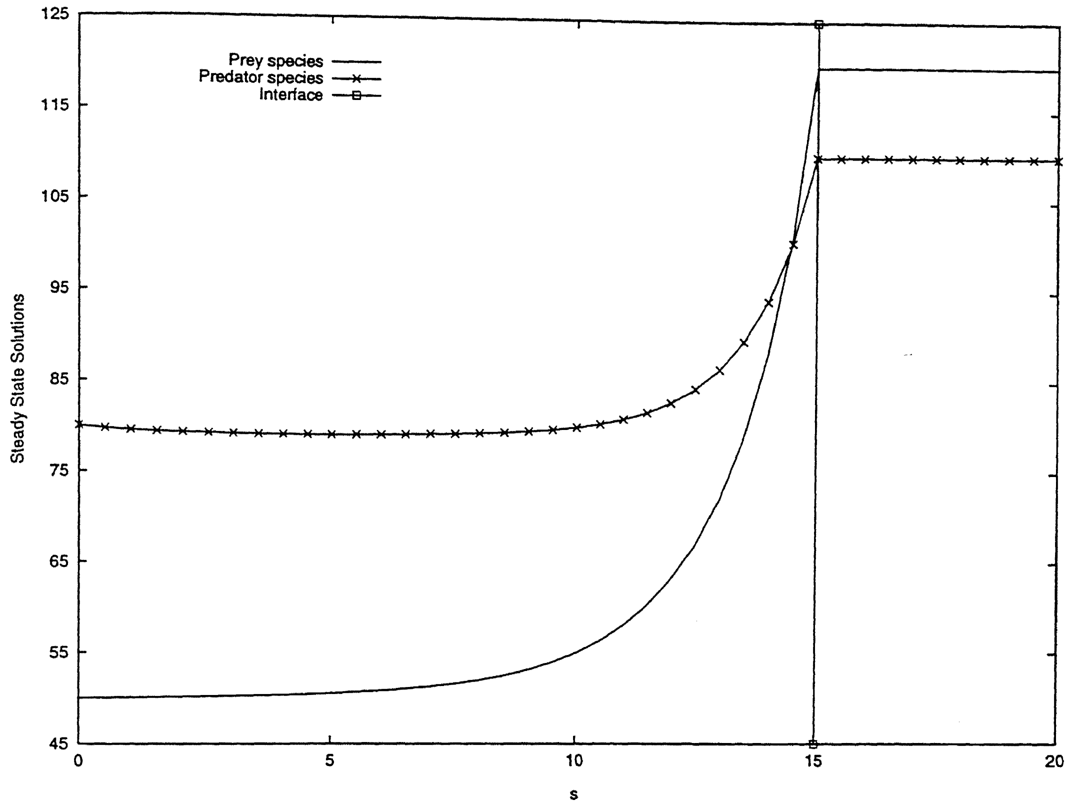


Figure 4.7: Effects of diffusion coefficients on the steady state solutions, for three set of values of D_{ij}'s.
Solid curves for D_{ij}'s = 0.04, dotted curves for D_{ij}'s = 0.40, Marked solid curves for D_{ij}'s = 2.00, for $b_i = 1.000E-6$, $\gamma_i = 1.0$, $i = 1, 2$ and

$r_1 = 0.01$, $K_1 = 50$, $\alpha_1 = 2.000E-05$, $a_1 = 0.5$
$r_2 = 0.02$, $K_2 = 100.5$, $\alpha_2 = 2.000E-05$, $a_2 = 0.5$
$s_1 = 0.02$, $M_1 = 100$, $\alpha_1 = 2.000E-05$, $a_1 = 0.5$
$s_2 = 0.03$, $M_2 = 150$, $\alpha_2 = 2.000E-05$, $a_2 = 0.5$



igure 4.8: The Steady State distributions when the both the species have uniform equi-
ibrium state ($K_2 = x_2^* = 120$, $M_2 = y_2^* = 110$) in the second patch.
$r_1 = 0.174$, $K_1 = 58$, $\alpha_1 = 2.0000E-04$, $a_1 = 0.2$
$s_1 = 0.316$, $M_1 = 79$, $\alpha_2 = 2.0000E-05$, $a_1 = 0.2$
$D_1 = 0.7$ $D_2 = 0.6$, $b_i = 1.0000E-05$, $\gamma_i = 1.0$, $\forall i, j = 1, 2$.

4.6 Summary

In this chapter, a dynamical model for two logistically growing species with prey-predator type interaction with diffusion in a two-patch environment is studied by assuming the rate of change of density of the first species decreases as the second species increases and the growth rate density of the later increases with the increase of density of the former. This model is proposed by keeping in view the situation in Doon Valley (Uttar Pradesh, India) where the depletion of forest biomass has increased patchiness in this valley by growth of biomass dependent industrialization (population) [see Shukla et al. [25], Munn et al. [17] for detail information].

To understand the role of diffusion and patchiness the proposed model has been analyzed for both homogeneous and two patch habitats. In absence of patchiness in the habitat an equilibrium which is stable locally as well as globally without diffusion under certain conditions remains stable under the same set of conditions with diffusion. However if an equilibrium is unstable it may become stable with diffusion in the homogeneous habitat under a certain condition. In the case with diffusion in two patch habitat the uniform steady state remains stable under two similar conditions as in the case of homogeneous habitat with diffusion.

In the case of non-uniform steady state, it is shown that there exists a positive, monoonic, continuous steady state solution with continuous flux at the interface of two adjoining patches, under both the reservoir and no-flux boundary conditions, for each species, that is symptotically stable in the linear and non-linear cases under some conditions. Also when the steady state solutions of both the species are non-uniform in the first patch and uniform in the second patch, then the stability of the system increases (decreases) as compared to the case of non-uniform (uniform) steady state in both the patches respectively. Thus it is concluded that patchiness, destabilizes the system.

Bibliography

1. **Comins, H.N.** and **Blatt, D.W.E.**, *Prey predator models in spatially heterogeneous environment*, J. Theoretical Biology.48, 75-83 (1974).

2. **Freedman, H.I.**, *Deterministic Mathematical Models in Population Ecology*, HIFR Consulting Ltd, Edmonton (1987).

3. **Freedman, H.I.**, *Graphical Stability, Enrichment and Pest Control by a Natural Enemy*, Mathl. Biosci. 31: 207-225 (1976).

4. **Freedman, H.I.** and **Shukla, J.B.**, *The effect of a predator resource on a diffusive predator-prey system,* Natural Resources Modeling, Volume 3, No.3, pp.359-383, Winter (1989).

5. **Freedman, H.I.**, **Shukla, J.B.** and **Takeuchi,Y.**, *Population Diffusion in a Two-Patch Environment*, Mathl. Biosci. 95: 111-123 (1989).

6. **Freedman, H.I.** and **Wu, J.**, *Steady-state analysis in a model for population diffusion in a multi-patch environment*, Nonlinear Analysis, Theory, Methods & Applications, Vol.18, No.6, pp. 517-542 (1992).

7. **Gopalsamy, K.**, *Competition, dispersion and co-existence*, Math. Bio. Science. 33, 25-33 (1977).

8. **Hallam, T.G.**, *A temporal study of diffusion effects on a population modelled by quadratic growth*, Non-linear Anal.Theory Methods Appl. 3: 123 - 133 (1979).

9. **Hastings, A.**, *Global stability in Lotka-Volterra systems with Diffusion*, J. Math. Biology 6, 163-168 (1978).

). **Hastings, A.**, *Dynamics of a Single Species in a Spatially Varying Environment: The Stabilizing Role of High Dispersal Rates*, J. Math. Biology 16, 49-55 (1982).

l. **Hsu, S.B.**, *On Global Stability of a Predator-Prey System*, Mathl. Biosci. 39, pp.1-10 (1978).

12. **Kerner, E.H.**, *Further considerations on statistical mechanics of biological associations*, Bull. of Math. Biophysics. 21, 217-255 (1959).

13. **Levin, S.A.**, *Population model and community structure in heterogeneous environments, in Mathematical Ecology*, T.G.Hallam and S.A.Levin,eds.,Springer,New York, pp. 295 - 321 (1986).

14. **Levin, S.A.**, *Spatial patterning and the structure of ecological communities*, Lectures on Mathematics in the Life Sciences, Vol. 8, (1976).

.5. **Levin, S.A.**, *Dispersion and population interactions*, Am. Nat. 108, 207-228 (1974).

.6. **McMurtrie, R.**, *Persistence and stability of single species and prey-predator system in spatially heterogeneous environments*, Mathl. Biosci. 39: 11-51 (1978).

.7. **Munn, R.E.** and **Fedorov, V.**, *The Environmental assessment, IIASA Project Report*, Vol.1, International Institute for Applied Systems Analysis, Laxenburg, Austria.

8. **Nallaswamy, R.** and **Shukla, J.B.**, *Effects of dispersal on the stability of a Prey-Predator system with functional response*, Mathl. Biosci. 60: pp. 123-132 (1982).

9. **Okubo, A.**, *Diffusion and Ecological Problem: Mathematical models*, Springer-Verlag, Berlin Heidelberg New York (1980).

0. **Pacala, S.W.** and **Roughgarden, J.**, *Spatial heterogeneity and interspecific competition*, Theor. Pop. Biol. 21: 92-113 (1982).

1. **Pao, C.V.**, *Coexistence and stability of a competition diffusion system in population dynamics*, J. Math. Anal. Appl. 83: 54-76 (1981).

2. **Rothe, F.**, *Global Solution of Reaction-Diffusion Systems*, Lecture Notes in Math., 1072, Springer-Verlag Berlin Heidelberg New York Tokyo 1984.

3. **Segel, L.A.**, **Jackson, J.L.**, *Dissipative structure: An explanation and an ecological example*, J. Theor. Biol. 37, 545-559 (1972).

4. **Shigesada, N.** and **Roughgarden, J.**, *The role of rapid dispersal in the population dynamics of competition*, Theor. Pop. Biol. 21: 353 - 372 (1982).

5. **Shukla, J.B.**, **Freedman, H.I.**, **Pal, V.N.**, **Mishra, O.P.**, **Agarwal, M.** and **Shukla, A.**, *Degradation and subsequent regeneration of a resource: A mathematical model*, Ecological Modelling, 44: 219-229, (1989).

. **Shukla, J.B.** and **Verma, S.**,*Effect of convective and dispersive interactions on the stability of two species*, Bul. Math. Biol. 43, 593-610, (1981).

7. **Shukla, V.P., Shukla, J.B.**, *Multispecies food webs with diffusion*, J. Math. Biol. 13, 339-344, (1982).

3. **Shukla, V.P., Shukla, J.B.** and **Das, P.C.**, *Environmental effects on the linear stability of a three species food chain model*, Mathl. Biosci. 57, 35-58, (1981).

). **Skellam, J.G.**, *Random dispersal in theoretical populations*, Biometrika 36: pp.199-218, (1951).

). **Smith, O.L.**, *The influence of environment gradients on ecosystem stability*, Am. Nat. 116: 1-24, (1980).

l. **Timm, U.** and **Okubo, A.**, *Diffusion-driven instability in a predator-prey system with time-varying diffusivities*, J. Math. Biol. 30: 307-320, (1992).

2. **Turing, A.M.**, *The chemical basis of morphogenesis*, Phil. Trans. Roy. Soc. London B237, 37-72, (1952).

3. **Williams, S.A.** and **Chow, Pao-Liu**, *Nonlinear Reaction-Diffusion Models for Interacting Populations*, J. Math. Anal. Appl. 62, 157-169 (1978).

Chapter 5

A Prey-Predator Type Model with Diffusion and a Supplementary Resource for the Prey in a Two-Patch Habitat

5.1 Introduction

As mentioned in chapter 4, an interesting problem in mathematical ecology is to study the growth and co-existence of species with diffusion in both homogeneous and patchy habitats. As noted before that diffusion, when it occurs, plays the role of increasing stability in a system of interacting populations [5, 7, 19, 20, 21, 23]. Levin [12, 13] has given elaborate survey of models with diffusion in both homogeneous and heterogeneous environment. McMurtrie [14], has also surveyed the literature related to populations model with diffusion and reported the effects of dispersal and spatial heterogeneity on stability of both single species and for Predator-Prey system. Nallaswamy and Shukla [17], considered a prey-predator model with functional response and diffusion and have shown, that if the equilibrium state is linearly stable, a subregion of the positive quadrant can be found in the phase plane where it is non-linearly stable with or without diffusion.

It may be noted here that in the above study the role of alternative or supplementary resource on equilibrium levels of populations as well as on their stability has not been discussed, although the study of resource-based interacting population biology is an interesting area of research in population dynamics. Some experimental investigations on micro-organisms using the chemostat [8, 18] have been conducted and perhaps the best laboratory idealization of nature for population studies has been described in [24]. Several mathematical models of such systems, involving competition and other types of non-interacting populations which depend upon growth limiting nutrient in a chemostat with constant input and variable washout rates have been studied [1, 10, 11]. Also some other mathematical investigations related to two competing populations which are wholly dependent on a self-renewable resource in a habitat without diffusion have been presented [6, 9, 15]. But very little attention has been given in the resource-based prey-predator system with diffusion, Freedman and Shukla [2], have studied the effect of a predator resource on a diffusive Predator-Prey system, showing the stabilizing role of diffusion.

In this chapter, we, therefore, study a logistically growing two species prey-predator type model with a self-renewable supplementary resource for prey population and diffusion in a two-patch habitats and discuss the stability of both the linear and nonlinear systems, under both the reservoir and no-flux boundary conditions. The model is proposed by keeping in view the depletion of forest resources due to increased forest resource dependent or independent industrialization and population causing patchiness in the Doon Valley, situated at the foot hills of Himalayas in India and affecting its biodiversity, Shukla et al. [22].

This chapter is organized as follows, first we write the prey-predator model with a self-renewable supplementary resource for the prey in a two-patch habitat. Next section, we study our main model in a two-patch habitat for both non-uniform and uniform steady state cases under both reservoir and no-flux boundary conditions.

5.2 Mathematical Model

We consider a dynamic model of two logistically growing animal (such as deer and wolf) species with prey-predator type interaction and diffusion in a two-patch forest habitat by assuming that the predator species uses the prey species as an alternative resource. In such a case the rate of change of density of the prey species decreases due increase in the density of the predator species, but its density increases due to the increase in the density of the prey species in both the patches. We also consider that there is a supplementary self-renewable resource for the prey species such that its density increases as the density of the resource biomass increases but the density of the resource biomass correspondingly decreases. Let $R_i(s,t)$, $x_i(s,t)$ and $y_i(s,t)$, $i = 1, 2$ be the densities of resource biomass, prey and predator species in the i-th patch respectively. Assuming that the resource biomass is non-diffusing, the model governing the system can be written as follows:

$$\frac{\partial R_i}{\partial t} = a_i R_i(1 - \frac{R_i}{C_i}) - \alpha_i R_i x_i \tag{5.1}$$

$$\frac{\partial x_i}{\partial t} = x_i \mathbf{g}_i(x_i) - y_i \mathbf{p}_i(x_i) + \theta\alpha_i R_i x_i + D_{1i}\frac{\partial^2 x_i}{\partial s^2} \tag{5.2}$$

$$\frac{\partial y_i}{\partial t} = y_i \mathbf{f}_i(y_i) + \gamma_i y_i \mathbf{p}_i(x_i) + D_{2i}\frac{\partial^2 y_i}{\partial s^2} \tag{5.3}$$

$$0 \leq s \leq L_2, \quad \text{and} \quad i = 1, 2.$$

where the i-th patch is assumed to lie along the spatial length $L_{i-1} \leq s \leq L_i$ $(L_0 = 0)$, C_i $(i = 1, 2)$ is the carrying capacity of the supplementary resource in the i-th patch and θ is the conversion rate of biomass density by the prey population assumed as constant. The functions $\mathbf{g}_i(x_i)$ and $\mathbf{f}_i(y_i)$ are the respective specific growth rates of prey and predator populations, $\mathbf{p}_i(x_i)$ is the interaction rate (predator response functions) and D_{1i}, D_{2i} are the diffusion coefficient of x_i and y_i in the i-th patch respectively. The constants α_i, $i = 1, 2$ are positive interaction rate coefficients of the prey species with the supplementary resource and γ_i, $i = 1, 2$ are conversion rate coefficients.

We assume the following assumption for $\mathbf{g}_i(x_i)$, $\mathbf{f}_i(y_i)$, and $\mathbf{p}_i(x_i)$:

AH_1: $\mathbf{g}_i(x_i),\ \mathbf{f}_i(y_i),\ \mathbf{p}_i(x_i)\ \in C^2[0,\infty)$

$\mathbf{g}_i(0) > 0,\ \mathbf{f}_i(0) > 0,\ \mathbf{p}_i(0) = 0$

For $x_i > 0$, $\mathbf{g}_i'(x_i) \leq 0,\ \mathbf{p}_i'(x_i) > 0$

For $y_i > 0$, $\mathbf{f}_i'(y_i) \leq 0$

When the environment has a carrying capacity K_i and M_i respectively for prey and predator populations in the i-th patch, then $\mathbf{g}_i(K_i) = 0$, $\mathbf{f}_i(M_i) = 0$, for $i = 1, 2$. Further we assume that,

AH_2: $\exists\ R_i^*, x_i^{**}, y_i^{**} > 0$, such that

$R_i^* = C_i[a_i - \alpha_i x_i^{**}]/a_i$

$x_i^{**}\mathbf{g}_i(x_i^{**}) - y_i^{**}\mathbf{p}_i(x_i^{**}) + \theta\alpha_i R_i^* x_i^{**} = 0$

$\mathbf{f}_i(y_i^{**}) + \gamma_i\mathbf{p}_i(x_i^{**}) = 0$

The model is studied under two set of boundary conditions i.e. reservoir and no-flux. In the case of reservoir boundary conditions, we take

$$x_1(0,t) = x_1^{**}\ ,\ x_2(L_2,t) = x_2^{**} \tag{5.4}$$

$$y_1(0,t) = y_1^{**}\ ,\ y_2(L_2,t) = y_2^{**} \tag{5.5}$$

and in the case of no-flux boundary conditions, we consider,

$$\frac{\partial x_1(0,t)}{\partial s} = 0 = \frac{\partial x_2(L_2,t)}{\partial s} \tag{5.6}$$

$$\frac{\partial y_1(0,t)}{\partial s} = 0 = \frac{\partial y_2(L_2,t)}{\partial s}. \tag{5.7}$$

We also assume the continuity and flux matching conditions at the interface $s = L_1$. The continuity conditions at the interface $s = L_1$ are,

$$x_1(L_1,t) = x_2(L_1,t),\ \ y_1(L_1,t) = y_2(L_1,t)\ \text{ and }\ R_1(L_1,t) = R_2(L_1,t) \tag{5.8}$$

and the continuous flux matching conditions at the interface $s = L_1$ for $x_i(s,t)$ and $y_i(s,t)$ are,

$$D_{11}\frac{\partial x_1(L_1,t)}{\partial s} = D_{12}\frac{\partial x_2(L_1,t)}{\partial s} \tag{5.9}$$

$$D_{21}\frac{\partial y_1(L_1,t)}{\partial s} = D_{22}\frac{\partial y_2(L_1,t)}{\partial s} \tag{5.10}$$

Finally the model is completed by assuming some positive initial distribution of each species, for $i = 1, 2$, that is,

$$x_i(s,0) = \chi_i(s) > 0, \; L_{i-1} < s < L_i \tag{5.11}$$

$$y_i(s,0) = \delta_i(s) > 0, \; L_{i-1} < s < L_i \tag{5.12}$$

$$R_i(s,0) = R_{0i}(s) > 0, \; L_{i-1} < s < L_i. \tag{5.13}$$

5.3 Analysis of the Model in Two-Patch Habitat

Our aim is to analyze the long time behavior of the system in both uniform and nonuniform cases in the following sections.

In next two subsections we will study the model (5.1)-(5.13), in the case of nonuniform steady state and the uniform state state respectively.

5.3.1 The Non-uniform Steady State: Under Both Sets of Boundary Conditions

Let u_i, v_i and w_i are the steady state solutions of the prey populations (x_i), predator populations (y_i) and the supplementary resource (R_i). Then the steady state system becomes:

$$w_i = \frac{C_i}{a_i}\left[a_i - \alpha_i u_i\right] \tag{5.14}$$

$$D_{1i}\frac{d^2u_i}{ds^2} + u_i\mathrm{g}_i(u_i) - v_i\mathrm{p}_i(u_i) + \theta\alpha_i w_i u_i = 0 \tag{5.15}$$

$$D_{2i}\frac{d^2v_i}{ds^2} + v_i\mathrm{f}_i(v_i) + \gamma_i v_i\mathrm{p}_i(u_i) = 0 \tag{5.16}$$

Now substituting the value of w_i from (5.14) into (5.15) and (5.16), we get,

$$D_{1i}\frac{d^2u_i}{ds^2} + u_i\mathcal{G}_i(u_i) - v_i\mathrm{p}_i(u_i) = 0 \tag{5.17}$$

$$D_{2i}\frac{d^2v_i}{ds^2} + v_i\mathrm{f}_i(v_i) + \gamma_i v_i\mathrm{p}_i(u_i) = 0 \tag{5.18}$$

where,

$$\mathcal{G}_i(u_i) = \mathrm{g}_i(u_i) + \theta\alpha_i\frac{C_i}{a_i}(a_i - \alpha_i u_i), \quad i = 1, 2$$

Since $\mathcal{G}_i(0) = \mathrm{g}_i(0) + C_i\theta\alpha_i > 0$ and $\mathcal{G}_i'(u_i) = \mathrm{g}_i'(u_i) - \frac{C_i\theta\alpha_i^2}{a_i} < 0$, for $i = 1, 2$. Hence the behavior the steady state system (5.17) and (5.18) with same set of boundary and matching conditions are identical with the steady state solutions of the previous chapter, i.e. the case when there is no supplementary resource for the prey populations, since the assumption $\mathbf{H_3}$ of the chapter 4, now modified as,
$\exists\ x_i^{**}, y_i^{**} > 0$, such that,

$$x_i^{**}\mathcal{G}_i(x_i^{**}) - y_i^{**}\mathrm{p}_i(x_i^{**}) = 0, \tag{5.19}$$

$$\mathrm{f}_i(y_i^{**}) + \gamma_i\mathrm{p}_i(x_i^{**}) = 0. \tag{5.20}$$

Also conditions (4.53) and (4.54) in this case modified as follows,

$$(x_i - x_i^{**})[x_i\mathcal{G}_i(x_i) - y_i\mathrm{p}_i(x_i)] < 0,\ \forall x_i \neq x_i^{**} \text{ and } min\{y_1^{**}, y_2^{**}\} \leq y_i \leq max\{y_1^{**}, y_2^{**}\} \tag{5.21}$$

$$(y_i - y_i^{**})[y_i\mathrm{f}_i(y_i) + \gamma_i y_i\mathrm{p}_i(x_i)] < 0,\ \forall y_i \neq y_i^{**} \text{ and } min\{x_1^{**}, x_2^{**}\} \leq x_i \leq max\{x_1^{**}, x_2^{**}\} \tag{5.22}$$

The analysis in the remaining part of this chapter we assuming these two conditions.
Remark: Since we are only interested on the positive steady state of the system. Therefore,

from (5.14), $u_i < a_i/\alpha_i$ and hence $\mathcal{G}_i(u_i) \geq \mathrm{g}_i(u_i)$, $\forall\ u_i$. Now, from (5.19) and (5.20), we get,

$$y_i^{**} = \frac{x_i^{**}\mathcal{G}_i(x_i^{**})}{\mathrm{p}_i(x_i^{**})} > y_i^*, \quad \text{and } x_i^{**} > x_i^*,$$

where x_i^* and y_i^* satisfy the following equations of chapter-4 [see (4.3) and (4.4)],

$$x_i^*\mathrm{g}_i(x_i^*) - y_i^*\mathrm{p}_i(x_i^*) = 0, \tag{5.23}$$

$$\mathrm{f}_i(y_i^*) + \gamma_i\mathrm{p}_i(x_i^*) = 0. \tag{5.24}$$

Hence in presence of a supplementary resource for the prey population, the level of steady state solutions of both the species are higher at each location in the habitat. It is shown numerically in Fig.5.1 [see section 5.4].

Now exactly in similar manner as the statement and proof of Theorem 4.4.4, 4.4.5 for reservoir boundary conditions we can state the following theorem without proof.

Theorem 5.3.1 *(i) There exists a positive, continuous, monotonic solution of system (5.17) with continuous flux at L_1.*

(ii) There exists a positive, continuous, monotonic solution of system (5.18) with continuous flux at L_1.

Now we consider the stability analysis of the system (5.1)-(5.3), (5.8)-(5.13) with reservoir boundary conditions (5.4) and (5.5). First we state the local stability of the system by the following theorem,

Theorem 5.3.2 *The steady-state, continuous, monotonic solutions of the linearized system (5.1)-(5.3) with reservoir boundary conditions and continuous flux at the interface $s = L_1$ is asymptotically stable provided the following conditions are satisfied:*

$$(i) \qquad \mathcal{X}_i \leq 0,\ \mathcal{Y}_i \leq 0,\ \mathcal{Z}_i \leq 0 \tag{5.25}$$

$$(ii) \quad \mathcal{U}_i^2 \leq 4\mathcal{X}_i\mathcal{Y}_i \tag{5.26}$$

$$(iii) \quad \mathcal{X}_i\mathcal{Y}_i\mathcal{Z}_i \leq \mathcal{Y}_i\mathcal{W}_i^2 + \mathcal{Z}_i\mathcal{U}_i^2. \tag{5.27}$$

where,

$$\mathcal{X}_i = \mathrm{g}_i(u_i) + u_i\mathrm{g}_i'(u_i) - v_i\mathrm{p}_i'(u_i) + \theta\alpha_i w_i, \quad \mathcal{Y}_i = \mathrm{f}_i(v_i) + v_i\mathrm{f}_i'(v_i) + \gamma_i\mathrm{p}_i(u_i),$$

$$\mathcal{Z}_i = a_i\left(1 - \frac{2w_i}{C_i}\right) - \alpha_i u_i, \quad \mathcal{U}_i = \frac{1}{2}[\gamma_i v_i\mathrm{p}_i'(u_i) - \mathrm{p}_i(u_i)], \quad \mathcal{W}_i = \frac{\alpha_i}{2}[\theta u_i - w_i],$$

for $x_1^{**} \leq u_i \leq x_2^{**}$, $y_1^{**} \leq v_i \leq y_2^{**}$, *where* x_i^{**} *and* y_i^{**} *are given by (5.19) and (5.20), for* $i = 1, 2$.

Proof: Linearizing (5.1), (5.2) and (5.3) by using,

$$R_i(s,t) = w_i(s) + r_i(s,t) \tag{5.28}$$

$$x_i(s,t) = u_i(s) + n_i(s,t) \tag{5.29}$$

$$y_i(s,t) = v_i(s) + m_i(s,t) \tag{5.30}$$

we have,

$$\frac{\partial r_i}{\partial t} = r_i\left[a_i\left(1 - \frac{2w_i}{C_i}\right) - \alpha_i u_i\right] - n_i\alpha_i w_i \tag{5.31}$$

$$\frac{\partial n_i}{\partial t} = n_i[\mathrm{g}_i(u_i) + u_i\mathrm{g}_i'(u_i) - v_i\mathrm{p}_i'(u_i) + \theta\alpha_i w_i] - m_i\mathrm{p}_i(u_i) + r_i\theta\alpha_i u_i + D_{1i}\frac{\partial^2 n_i}{\partial s^2} \tag{5.32}$$

$$\frac{\partial m_i}{\partial t} = m_i[\mathrm{f}_i(v_i) + v_i\mathrm{f}_i'(v_i) + \gamma_i\mathrm{p}_i(u_i)] + n_i\gamma_i v_i\mathrm{p}_i'(u_i) + D_{2i}\frac{\partial^2 m_i}{\partial s^2} \tag{5.33}$$

Using (5.28), (5.29) and (5.30) the corresponding boundary and matching conditions can be obtained as follows

$$n_1(0,t) = 0 = n_2(L_2,t), \quad m_1(0,t) = 0 = m_2(L_2,t)$$

$$n_1(L_1,t) = n_2(L_1,t), \quad m_1(L_1,t) = m_2(L_1,t)$$

$$D_{11}\frac{\partial n_1}{\partial s}(L_1,t) = D_{12}\frac{\partial n_2}{\partial s}(L_1,t), \quad D_{21}\frac{\partial m_1}{\partial s}(L_1,t) = D_{22}\frac{\partial m_2}{\partial s}(L_1,t).$$

Now we consider the following positive definite function,

$$V(t) = \sum_{1}^{2} \int_{L_{i-1}}^{L_i} \frac{1}{2}[n_i^2 + m_i^2 + r_i^2]ds \tag{5.34}$$

Differentiating (5.34)w.r.t. t, we get,

$$\dot{V}(t) = \sum_{1}^{2} \int_{L_{i-1}}^{L_i} \left[n_i \frac{\partial n_i}{\partial t} + m_i \frac{\partial m_i}{\partial t} + r_i \frac{\partial r_i}{\partial t} \right] ds$$

By using (5.31), (5.32) and (5.33), we get,

$$\begin{aligned}
\dot{V}(t) = \quad & \sum_{1}^{2} \int_{L_{i-1}}^{L_i} n_i^2 [\mathrm{g}_i(u_i) + u_i \mathrm{g}_i'(u_i) - v_i \mathrm{p}_i'(u_i) + \theta \alpha_i w_i] ds \\
+ \quad & \sum_{1}^{2} \int_{L_{i-1}}^{L_i} m_i^2 [\mathrm{f}_i(v_i) + v_i \mathrm{f}_i'(v_i) + \gamma_i \mathrm{p}_i(u_i)] ds \\
+ \quad & \sum_{1}^{2} \int_{L_{i-1}}^{L_i} r_i^2 \left[a_i \left(1 - \frac{2w_i}{C_i}\right) - \alpha_i u_i \right] ds \\
+ \quad & \sum_{1}^{2} \int_{L_{i-1}}^{L_i} n_i m_i [-\mathrm{p}_i(u_i) + \gamma_i v_i \mathrm{p}_i'(u_i)] ds + \sum_{1}^{2} \int_{L_{i-1}}^{L_i} n_i r_i \alpha_i [\theta u_i - w_i] ds \\
+ \quad & \sum_{1}^{2} D_{1i} \int_{L_{i-1}}^{L_i} n_i \frac{\partial^2 n_i}{\partial s^2} ds + \sum_{1}^{2} D_{2i} \int_{L_{i-1}}^{L_i} m_i \frac{\partial^2 m_i}{\partial s^2} ds
\end{aligned}$$

Therefore,

$$\begin{aligned}
\dot{V}(t) = \quad & \sum_{1}^{2} \int_{L_{i-1}}^{L_i} [\mathcal{X}_i n_i^2 + \mathcal{Y}_i m_i^2 + \mathcal{Z}_i r_i^2 + 2\mathcal{U}_i n_i m_i + 2\mathcal{W}_i r_i n_i] ds \\
- \quad & \sum_{1}^{2} D_{1i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial n_i}{\partial s} \right)^2 ds - \sum_{1}^{2} D_{2i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial m_i}{\partial s} \right)^2 ds
\end{aligned} \tag{5.35}$$

where the functions $\mathcal{X}_i$, $\mathcal{Y}_i$, $\mathcal{Z}_i$, $\mathcal{U}_i$, and $\mathcal{W}_i$ are as follows,

$$\mathcal{X}_i = \mathrm{g}_i(u_i) + u_i \mathrm{g}_i'(u_i) - v_i \mathrm{p}_i'(u_i) + \theta \alpha_i w_i, \quad \mathcal{Y}_i = \mathrm{f}_i(v_i) + v_i \mathrm{f}_i'(v_i) + \gamma_i \mathrm{p}_i(u_i),$$

$$\mathcal{Z}_i = a_i \left(1 - \frac{2w_i}{C_i}\right) - \alpha_i u_i, \quad \mathcal{U}_i = \frac{1}{2}[\gamma_i v_i \mathrm{p}_i'(u_i) - \mathrm{p}_i(u_i)], \quad \mathcal{W}_i = \frac{\alpha_i}{2}[\theta u_i - w_i]$$

Hence $\dot{V}$ is negative definite if the conditions (5.25), (5.26) and (5.27) stated in theorem are satisfied, for both $i = 1, 2$. ∎

In the following we state the nonlinear stability conditions for the system.

Theorem 5.3.3 *The steady-state, continuous, monotonic solutions of nonlinear system (5.1)-(5.3), (5.8)-(5.13) with reservoir boundary conditions (5.4)-(5.5) is asymptotically stable in the subregion of* $\mathbf{R}$: $\{x_1^{**} \leq x_i,\ u_i \leq x_2^{**},\ y_1^{**} \leq y_i,\ v_i \leq y_2^{**},\ for\ i = 1, 2\}$ *provided the following conditions are satisfied:*

$$(i) \quad \mathcal{N}_{xi} \leq 0,\ \mathcal{N}_{yi} \leq 0,\ \mathcal{N}_{zi} \leq 0 \tag{5.36}$$

$$(ii) \quad \mathcal{N}_{ui}^2 \leq 4\mathcal{N}_{xi}\mathcal{N}_{yi} \tag{5.37}$$

$$(iii) \quad \mathcal{N}_{xi}\mathcal{N}_{yi}\mathcal{N}_{zi} \leq \mathcal{N}_{yi}\mathcal{N}_{wi}^2 + \mathcal{N}_{zi}\mathcal{N}_{ui}^2. \tag{5.38}$$

where

$$\begin{aligned}
\mathcal{N}_{xi} &= \frac{x_i \mathrm{g}_i(x_i) - u_i \mathrm{g}_i(u_i)}{x_i - u_i} - y_i \frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(u_i)}{x_i - u_i} + \theta \alpha_i R_i, \\
\mathcal{N}_{yi} &= \frac{y_i \mathrm{f}_i(y_i) - v_i \mathrm{f}_i(v_i)}{y_i - v_i} + \gamma_i \mathrm{p}_i(u_i) \\
\mathcal{N}_{zi} &= a_i \left(1 - \frac{R_i + w_i}{C_i}\right) - \alpha_i u_i, \\
\mathcal{N}_{ui} &= \frac{1}{2}\left[\gamma_i y_i \frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(u_i)}{x_i - u_i} - \mathrm{p}_i(u_i)\right] \\
\mathcal{N}_{wi} &= \frac{\alpha_i}{2}[\theta u_i - R_i].
\end{aligned} \tag{5.39}$$

Proof: By using (5.28), (5.29) and (5.30), we get from (5.1), (5.2) and (5.3),

$$\frac{\partial r_i}{\partial t} = r_i \left[a_i \left(1 - \frac{R_i + w_i}{C_i}\right) - \alpha_i u_i\right] - n_i \alpha_i R_i \tag{5.40}$$

$$\frac{\partial n_i}{\partial t} = n_i \left[\frac{x_i \mathrm{g}_i(x_i) - u_i \mathrm{g}_i(u_i)}{x_i - u_i} - y_i \frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(u_i)}{x_i - u_i} + \theta \alpha_i R_i\right] - m_i \mathrm{p}_i(u_i) + r_i \theta \alpha_i u_i + D_{1i} \frac{\partial^2 n_i}{\partial s^2} \tag{5.41}$$

$$\frac{\partial m_i}{\partial t} = m_i \left[\frac{y_i \mathrm{f}_i(y_i) - v_i \mathrm{f}_i(v_i)}{y_i - v_i} + \gamma_i \mathrm{p}_i(u_i)\right] + n_i \left[\gamma_i y_i \frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(u_i)}{x_i - u_i}\right] + D_{2i} \frac{\partial^2 m_i}{\partial s^2} \tag{5.42}$$

Here also we consider the same positive definite function as in the case of linear stability.

$$V(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \frac{1}{2}[n_i^2 + m_i^2 + r_i^2]ds$$

From which we get,

$$\dot{V}(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \left[n_i \frac{\partial n_i}{\partial t} + m_i \frac{\partial m_i}{\partial t} + r_i \frac{\partial r_i}{\partial t} \right] ds$$

By using (5.40), (5.41) and (5.42), we get,

$$\begin{aligned} \dot{V}(t) = & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2 \left[\frac{x_i \mathrm{g}_i(x_i) - u_i \mathrm{g}_i(u_i)}{x_i - u_i} - y_i \frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(u_i)}{x_i - u_i} + \theta \alpha_i R_i \right] ds \\ + & \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2 \left[\frac{y_i \mathrm{f}_i(y_i) - v_i \mathrm{f}_i(v_i)}{y_i - v_i} + \gamma_i \mathrm{p}_i(u_i) \right] ds \\ + & \sum_1^2 \int_{L_{i-1}}^{L_i} r_i^2 \left[a_i \left(1 - \frac{R_i + w_i}{C_i} \right) - \alpha_i u_i \right] ds \\ + & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i \left[\gamma_i y_i \frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(u_i)}{x_i - u_i} - \mathrm{p}_i(u_i) \right] ds + \sum_1^2 \int_{L_{i-1}}^{L_i} r_i n_i \alpha_i [\theta u_i - R_i] ds \\ + & \sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} n_i \frac{\partial^2 n_i}{\partial s^2} ds + \sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} m_i \frac{\partial^2 m_i}{\partial s^2} ds \end{aligned}$$

Therefore,

$$\begin{aligned} \dot{V}(t) = & \sum_1^2 \int_{L_{i-1}}^{L_i} [\mathcal{N}_{xi} n_i^2 + \mathcal{N}_{yi} m_i^2 + \mathcal{N}_{zi} r_i^2 + 2\mathcal{N}_{ui} n_i m_i + 2\mathcal{N}_{wi} r_i n_i] ds \\ - & \sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial n_i}{\partial s} \right)^2 ds - \sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial m_i}{\partial s} \right)^2 ds \end{aligned} \tag{5.43}$$

where the functions $\mathcal{N}_{xi}$, $\mathcal{N}_{yi}$, $\mathcal{N}_{zi}$, $\mathcal{N}_{ui}$ and $\mathcal{N}_{wi}$ are given by (5.39). Hence $\dot{V}$ is negative definite if the conditions (5.36)-(5.38) holds, for both $i = 1, 2$.

It is noted that if we linearize the conditions of theorem 5.3.3, we get the conditions of theorem 5.3.2.

Same results as discussed above for reservoir boundary conditions are also true for the system (5.1)-(5.3), (5.8)-(5.13) with no-flux boundary conditions (5.6) and (5.7).

5.3.2 The Uniform Equilibrium State: Under Both Sets of Boundary Conditions

The main purpose of this section is to find the conditions for local and global stability of the uniform equilibrium state, i.e. $x_i(s,t) \equiv K^*$, $y_i(s,t) \equiv M^*$ and $R_i(s,t) \equiv C^*$, for $0 \leq s \leq L_2$, $t \geq 0$, of the system, under both sets of boundary conditions.

Theorem 5.3.4 *The equilibrium (C^*, K^*, M^*) is locally asymptotically stable, if the following conditions are satisfied,*

$$H_i^* + \theta\alpha_i C^* \leq 0, \quad i = 1, 2, \tag{5.44}$$

and

$$[\gamma_i M^* \mathrm{p}_i'(K^*) - \mathrm{p}_i(K^*)]^2 \leq 4[H_i^* + \theta\alpha_i C^*][M^* \mathrm{f}_i'(M^*)], \quad i = 1, 2 \tag{5.45}$$

where H_i^* is given by

$$H_i^* = \mathrm{g}_i(K^*) + K^* \mathrm{g}_i'(K^*) - M^* \mathrm{p}_i(K^*) \tag{5.46}$$

Proof: Lineariazing the system (5.1)-(5.3), by using

$$\begin{aligned} R_i(s,t) &= C^* + r_i(s,t) && (5.47) \\ x_i(s,t) &= K^* + n_i(s,t) && (5.48) \\ y_i(s,t) &= M^* + m_i(s,t) && (5.49) \end{aligned}$$

we get,

$$\frac{\partial r_i}{\partial t} = r_i \left[-\frac{a_i C^*}{C_i} \right] - n_i \alpha_i C^* \tag{5.50}$$

$$\frac{\partial n_i}{\partial t} = n_i[\mathrm{g}_i(K^*)+K^*\mathrm{g}_i'(K^*)-M^*\mathrm{p}_i'(K^*)+\theta\alpha_i C^*]-m_i\mathrm{p}_i(K^*)+r_i\theta\alpha_i K^*+D_{1i}\frac{\partial^2 n_i}{\partial s^2} \quad (5.51)$$

$$\frac{\partial m_i}{\partial t} = m_i M^*\mathrm{f}_i'(M^*) + n_i\gamma_i M^*\mathrm{p}_i'(K^*) + D_{2i}\frac{\partial^2 m_i}{\partial s^2} \quad (5.52)$$

Considering the following positive definite function,

$$V = \frac{1}{2}\sum_1^2 \int_{L_{i-1}}^{L_i} \left[(x_i - K^*)^2 + (y_i - M^*)^2 + d_i(R_i - C^*)^2\right] \quad (5.53)$$

where d_i, $i = 1, 2$ are positive constants.

Differentiating (5.53) and using (5.50)-(5.52), we get

$$\begin{aligned}
\dot{V} = \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2[H_i^* + \theta\alpha_i C^*]ds + \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2 M^*\mathrm{f}_i'(M^*)ds + \sum_1^2 \int_{L_{i-1}}^{L_i} r_i^2\left[-\frac{d_i a_i C^*}{C_i}\right]ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i[-\mathrm{p}_i(K^*) + \gamma_i M^*\mathrm{p}_i'(K^*)]ds + \sum_1^2 \int_{L_{i-1}}^{L_i} n_i r_i[\alpha_i\{\theta K^* - d_i C^*\}]ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} D_{1i} n_i \frac{\partial^2 n_i}{\partial s^2}ds + \sum_1^2 \int_{L_{i-1}}^{L_i} D_{2i} m_i \frac{\partial^2 m_i}{\partial s^2}ds
\end{aligned} \quad (5.54)$$

Again, using integration by parts, for both type of boundary conditions, we get,

$$\begin{aligned}
\sum_1^2 \int_{L_{i-1}}^{L_i} D_{1i} n_i \frac{\partial^2 n_i}{\partial s^2}ds &= -\sum_1^2 D_{1i}\int_{L_{i-1}}^{L_i}\left(\frac{\partial n_i}{\partial s}\right)^2 ds \\
\sum_1^2 \int_{L_{i-1}}^{L_i} D_{2i} m_i \frac{\partial^2 m_i}{\partial s^2}ds &= -\sum_1^2 D_{2i}\int_{L_{i-1}}^{L_i}\left(\frac{\partial m_i}{\partial s}\right)^2 ds.
\end{aligned}$$

Choosing d_i, for $i = 1, 2$, such that, the coefficients of $n_i r_i$ become zero, i.e. $d_1 = d_2 = \theta K^*/C^*$. Therefore, from (5.54), $\dot{V}$ is negative definite, if the conditions (5.44) and (5.45) are satisfied. ∎

Moreover,

Theorem 5.3.5 *Let $H_i^* + \theta\alpha_i C^* > 0$. Then the equilibrium (C^*, K^*, M^*) is locally asymptotically stable, if the conditions (5.45) along with*

$$H_i^* + \theta\alpha_i C^* \le D_{1i}\frac{\pi^2}{(L_i - L_{i-1})^2},$$

for $i = 1, 2$, hold.

Proof: By using Poincare's Inequality, we get

$$D_{1i}\int_{L_{i-1}}^{L_i}\left[\frac{\partial n_i}{\partial s}\right]^2 ds \leq D_{1i}\frac{\pi^2}{(L_i-L_{i-1})^2}\int_{L_{i-1}}^{L_i} n_i^2 ds$$

Therefore from (5.54), we get,

$$\begin{aligned}\dot{V} \leq \quad & \sum_1^2\int_{L_{i-1}}^{L_i} n_i^2 x[H_i^* + \theta\alpha_i C^* - D_{1i}\frac{\pi^2}{(L_i-L_{i-1})^2}]ds + \sum_1^2\int_{L_{i-1}}^{L_i} m_i^2 M^*\mathrm{f}_i'(M^*)ds \\ + \quad & \sum_1^2\int_{L_{i-1}}^{L_i} r_i^2\left[-\frac{d_i a_i C^*}{C_i}\right]ds + \sum_1^2\int_{L_{i-1}}^{L_i} n_i m_i[-\mathrm{p}_i(K^*) + \gamma_i M^*\mathrm{p}_i'(K^*)]ds \\ - \quad & \sum_1^2 D_{2i}\int_{L_{i-1}}^{L_i}\left(\frac{\partial m_i}{\partial s}\right)^2 ds\end{aligned}$$

Hence the theorem.

We now state the following theorem for the global stability of the uniform steady state,

Theorem 5.3.6 *The uniform steady-state (C^*,K^*,M^*) is globally asymptotically stable if*

$$\mathcal{A}_i(x_i) = \frac{x_i\mathrm{g}_i(x_i) - M^*\mathrm{p}_i(x_i)}{x_i - K^*} + \theta\alpha_i C^* < 0, \quad \forall x_i \neq K^*. \tag{5.55}$$

$$\left[\gamma_i\frac{\mathrm{p}_i(x_i)-\mathrm{p}_i(K^*)}{x_i-K^*} - \frac{\mathrm{p}_i(x_i)}{x_i}\right]^2 \leq 4\frac{\mathcal{A}_i(x_i)}{x_i}\left[\frac{\mathrm{f}_i(y_i)-\mathrm{f}_i(M^*)}{y_i-M^*}\right], \tag{5.56}$$

and

$$\frac{\mathcal{A}_i(x_i)}{x_i}\left[\frac{\mathrm{f}_i(y_i)-\mathrm{f}_i(M^*)}{y_i-M^*}\right]\left[\frac{a_i}{C_i}\right] \leq \left[\frac{\mathrm{f}_i(M^*)-\mathrm{f}_i(y_i)}{y_i-M^*}\right]\left[\alpha_i^2(\theta-R_i)^2\right] + \frac{a_i}{C_i}\left[\frac{\mathcal{A}_i(x_i)}{x_i}\right]^2. \tag{5.57}$$

Proof: Let us consider the following positive definite function,

$$\begin{aligned}V(x,y,R) = \quad & \sum_1^2\int_{L_{i-1}}^{L_i}\left(x_i - K^* - K^* ln\frac{x_i}{K^*}\right)ds + \sum_1^2\int_{L_{i-1}}^{L_i}\left(y_i - M^* - M^* ln\frac{y_i}{M^*}\right)ds \\ & \sum_1^2\int_{L_{i-1}}^{L_i}\left(R_i - C^* - C^* ln\frac{R_i}{C^*}\right)ds\end{aligned} \tag{5.58}$$

Differentiating (5.58) with respect to t, and using (5.1)-(5.3) we get,

$$
\begin{aligned}
\dot{V}(s,t) = \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} \left(\frac{x_i - K^*}{x_i}\right) \frac{\partial x_i}{\partial t} ds + \sum_1^2 \int_{L_{i-1}}^{L_i} \left(\frac{y_i - M^*}{y_i}\right) \frac{\partial y_i}{\partial t} ds \\
& + \sum_1^2 \int_{L_{i-1}}^{L_i} \left(\frac{R_i - C^*}{R_i}\right) \frac{\partial R_i}{\partial t} ds \\
= \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} \frac{(x_i - K^*)^2}{x_i} \left[\frac{x_i \mathrm{g}_i(x_i) - M^* \mathrm{p}_i(x_i)}{x_i - K^*} + \theta \alpha_i C^*\right] ds \\
& + \sum_1^2 \int_{L_{i-1}}^{L_i} (y_i - y^*)^2 \left[\frac{\mathrm{f}_i(y_i) - \mathrm{f}_i(M^*)}{y_i - M^*}\right] ds - \sum_1^2 \int_{L_{i-1}}^{L_i} (R_i - C^*)^2 \left(-\frac{a_i}{C_i}\right) ds \\
& + \sum_1^2 \int_{L_{i-1}}^{L_i} (x_i - K^*)(y_i - M^*) \left[\gamma_i \frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(K^*)}{x_i - K^*} - \frac{\mathrm{p}_i(x_i)}{x_i}\right] ds \\
& + \sum_1^2 \int_{L_{i-1}}^{L_i} (x_i - K^*)(y_i - M^*) \alpha_i [\theta - R_i] ds \\
& + \sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} \frac{x_i - K^*}{x_i} \frac{\partial^2 x_i}{\partial s^2} ds + \sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} \frac{y_i - M^*}{y_i} \frac{\partial^2 y_i}{\partial s^2} ds
\end{aligned}
$$

Now consider the integrals, and using both set of boundary and flux matching conditions at the interface,

$$
[x_1(0,t) - K^*] \frac{\partial x_1}{\partial s}(0,t) = [x_2(L_2,t) - K^*] \frac{\partial x_2}{\partial s}(L_2,t) = 0 \tag{5.59}
$$

and

$$
[y_1(0,t) - M^*] \frac{\partial y_1}{\partial s}(0,t) = [y_2(L_2,t) - M^*] \frac{\partial y_2}{\partial s}(L_2,t) = 0 \tag{5.60}
$$

we get,

$$
\sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} \frac{x_i - K^*}{x_i} \frac{\partial^2 x_i}{\partial s^2} ds = -\sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} \frac{K^*}{x_i^2} \left(\frac{\partial x_i}{\partial s}\right)^2 ds \tag{5.61}
$$

and

$$
\sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} \frac{y_i - M^*}{y_i} \frac{\partial^2 y_i}{\partial s^2} ds = -\sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} \frac{M^*}{y_i^2} \left(\frac{\partial y_i}{\partial s}\right)^2 ds \tag{5.62}
$$

Now if the conditions (5.55) $\rightarrow$ (5.57) are satisfied, then $\dot{V}(x,y) < 0$, and $\dot{V}(C^*, K^*, M^*) = 0$. Therefore $\dot{V}(x,y)$ is negative definite over $R > 0$, $x > 0$, $y > 0$ with respect to $R_i^* = C^*$, $x_i^* = K^*$, $y_i^* = M^*$, proving the theorem. ∎

Remark: On comparing the analysis of this chapter with chapter-4 we may conclude that the role of supplementary resource is to increase the level of non-uniform steady state at each point of the habitat.

5.4 Numerical Example

Now, we discuss a numerical example to study the behavoir of the steady state solutions of the above system. The results of this section are compared with the case of a prey-predator system as discussed in chapter-4. For this we consider the following particular form of functions:

$$\mathrm{g}_i(u_i) = r_i\left(1 - \frac{u_i}{K_i}\right), \ \mathrm{f}_i(v_i) = s_i\left(1 - \frac{v_i}{M_i}\right), \ \mathrm{p}_i(u_i) = e_i u_i, \quad i = 1, 2$$

also for simplicity take, $C_1 = C_2 = C$. Then the steady state system (5.17) and (5.18), becomes

$$D_{1i}\frac{d^2 u_i}{ds^2} + u_i\left[r_i\left(1 - \frac{u_i}{K_i}\right) + \frac{\theta\alpha_i C}{a_i}(a_i - \alpha_i u_i)\right] - e_i v_i u_i = 0 \tag{5.63}$$

$$D_{2i}\frac{d^2 v_i}{ds^2} + s_i v_i\left(1 - \frac{v_i}{M_i}\right) + \gamma_i e_i v_i u_i = 0 \tag{5.64}$$

with reservoir boundary conditions

$$u_1(0) = x_1^{**}, u_2(L_2) = x_2^{**}, \quad \text{and} \tag{5.65}$$

$$v_1(0) = y_1^{**}, v_2(L_2) = y_2^{**}, \tag{5.66}$$

and the continuity and flux matching conditions at the interface $s = L_1$,

$$D_{11}\frac{du_1}{ds}(L_1) = D_{12}\frac{du_2}{ds}(L_1), \ D_{21}\frac{dv_1}{ds}(L_1) = D_{22}\frac{dv_2}{ds}(L_1), \text{ and} \tag{5.67}$$

$$u_1(L_1) = u_2(L_1), v_1(L_1) = v_2(L_1). \tag{5.68}$$

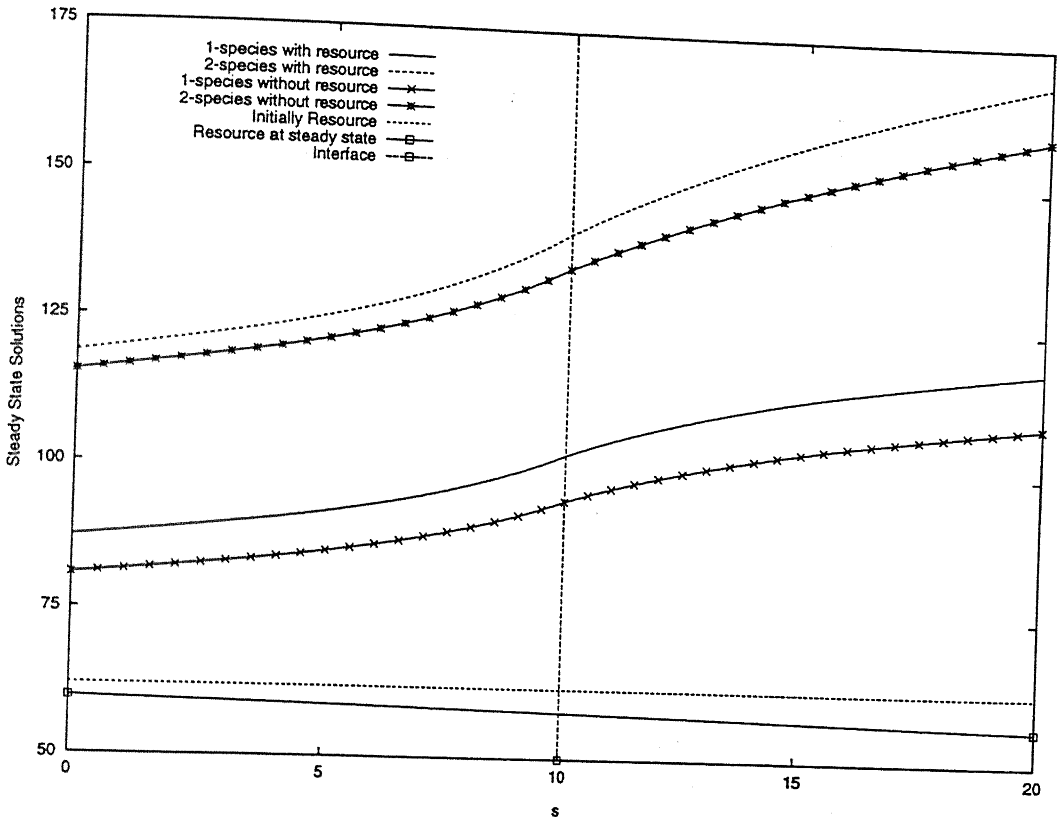


Figure 5.1: The steady state solutions for both the species, with and without supplementary resource for the prey

The equations (5.63)-(5.68) are numerically solved, for the following set of parameters, $L_1 = 10$, $L_1 = 20$, $D_{11} = 0.8$, $D_{12} = 0.9$, $D_{21} = 0.8$, $D_{22} = 0.9$, $r_1 = 0.03$, $r_2 = 0.025$, $a_1 = 1.0$, $a_2 = 1.0$, $s_1 = 0.03$, $s_2 = 0.01$, $e_1 = 5.0E - 05$, $e_2 = 5.0E - 05$, $K_1 = 100$, $K_2 = 125$, $M_1 = 75$, $M_2 = 50$, $\alpha_1 = 5.0E - 05$, $\alpha_2 = 2.0E - 05$, $C = 60$, $\gamma_1 = 0.4$, $\gamma_2 = 1.0$ and $\theta = 0.7$, and the solutions are shown in Fig.5.1. By using the above values of the parameters, we get, $x_1^{**} = 87.2 > x_1^* = 80.77$, $x_2^{**} = 118.58 > x_2^* = 109.09$, $y_1^{**} = 118.60 > y_1^* = 115.385$, and $y_2^{**} = 168.58 > y_2^* = 159.09$. It is noted from the figure that, in presence of a supplementary resource for the prey, the level of steady state distributions of both the prey and predator species are higher at each points of the habitat.

5.5 Summary

In chapter-4, we have discussed the existence and stability of the non-uniform steady state corresponding to a prey-predator system, where the predator species partially depends upon the prey species, in a two patch habitat with diffusion. In this chapter the same ecological problem is modelled and analyzed when there is a nondiffusing renewable resource for the prey population in both the patches. It has been assumed that both the prey and the predator population follow a general type of logistic growth in each of the patches as in the previous chapter. Also the self-renewable supplementary resource is logistically growing.

It is shown, in a similar manner as in chapter-4, that there exists a positive, monotonic, continuous steady state solution with continuous matching at the interface for both the species. We have also obtained the criteria for asymptotic stability both linear and nonlinear cases under both set of boundary conditions. It has been further shown that in presence of supplementary resource the level of steady state distribution of prey population increases and hence the level of steady state distribution of predator species also increases. It is shown that the effect of patchiness is destabilizing even in presence of a self-renewable supplementary resource for the prey species.

Bibliography

1. **Butler, G.J.** and **Wolkowicz**, *A mathematical model of the chemostat with a general class of functions describing nutrient uptake*, SIAM J. Appl. Math., Vol.45, No.1, (1985).

2. **Freedman, H.I.** and **Shukla, J.B.**, *The effect of a predator resource on a diffusive predator-prey system,* Natural Resources Modeling, Vol.3, No.3, 359-383, (1989).

3. **Freedman, H.I., Shukla, J.B.** and **Takeuchi,Y.**, *Population Diffusion in a Two-Patch Environment*, Mathl. Biosci., Vol.95, 111-123 (1989).

4. **Freedman, H.I.** and **Wu, J.**, *Steady-state analysis in a model for population diffusion in a multi-patch environment*, Nonlinear Analysis, Theory, Methods & Applications, Vol.18, No.6, 517-542 (1992).

5. **Gopalsamy, K.**, *Competition, dispersion and co-existence*, Math. Bio. Sci., Vol.33, 25-33 (1977).

6. **Gopalsamy, K.**, *Convergence in a resource-based competition system*, Bull. Math. Biol., Vol.48(5/6), 681-699, (1986).

7. **Hallam, T.G.**, *A temporal study of diffusion effects on a population modelled by quadratic growth*, Nonl. Anal. Theor. Methods & Appl., Vol.3, 123 - 133 (1979).

8. **Herbert, D., Elsworth** and **Telling, R.C.**, *The continuous culture of bacteria: a theoretical and experimental study*, J. Gen. Microbiology, Vol.4, 601-622, (1956).

9. **Hsu, S.B.**, *On a resource based ecological competition model with interference*, J. Math. Biol., Vol.12, 45-52, (1981).

10. **Hsu, S.B.**, *Limiting behavior for competing species*, SIAM J. Appl. Math., Vol.34(4), (1978).

11. **Hsu, S.B., Hubbell, S.P.** and **Waltman, P.**, *A mathematical theory of single-nutrient competitions in continuous cultures of microorganism*, SIAM J. Appl. Math., Vol.23, 366-383 (1977).

12. **Levin, S.A.**, *Spatial patterning and the structure of ecological communities*, Lectures on Mathematics in the Life Sciences, Vol.8, (1976).

13. **Levin, S.A.**, *Dispersion and population interactions*, Am. Nat., Vol.108, 207-228 (1974).

14. **McMurtrie, R.**, *Persistence and stability of single species and prey-predator system in spatially heterogeneous environments*, Mathl. Biosci., Vol.39, 11-51 (1978).

15. **Mitra, D, Mukherjee, D.** and **Roy, A.B.**, *Permanent coexistence in a resource-based competition system*, Ecol. Modelling Vol.60, 77-85 (1992).

16. **Munn, R.E.** and **Fedorov, V.**, *The Environmental assessment, IIASA Project Report*, Vol.1, International Institute for Applied Systems Analysis, Laxenburg, Austria.

17. **Nallaswamy, R.** and **Shukla, J.B.**, *Effects of dispersal on the stability of a Prey-Predator system with functional response*, Mathl. Biosci., Vol.60, 123-132 (1982).

18. **Novick, A.** and **Szilard, L.**, *Description of the chemostat*, Science, Vol.112, 715-716, (1950).

19. **Okubo, A.**, *Diffusion and Ecological Problem: Mathematical models*, Springer-Verlag, Berlin Heidelberg New York (1980).

20. **Pao, C.V.**, *Coexistence and stability of a competition diffusion system in population dynamics*, J. Math. Anal. Appl., Vol.83, 54-76 (1981).

21. **Rothe, F.**, *Global Solution of Reaction-Diffusion Systems*, Lecture Notes in Math.**1072**, Springer-Verlag Berlin Heidelberg New York Tokyo 1984.

22. **Shukla, J.B., Freedman, H.I., Pal, V.N., Mishra, O.P., Agarwal, M.** and **Shukla, A.**, *Degradation and subsequent regeneration of a resource: A mathematical model*, Ecol. Modelling, Vol.44, 219-229, (1989).

23. **Shukla, V.P., Shukla, J.B.**, *Multispecies food webs with diffusion*, J. Math. Biol., Vol.13, 339-344, (1982).

24. **Williams, F.M.**, *Dynamics of microbial populations*, Systems Analysis and Simulation in Ecology, B.Patten, ed., Academic Press, New York, Chapter-3, (1971).

Chapter 6

A Two Competing Species Model with Diffusion in Homogeneous and Two-Patch Habitats

6.1 Introduction

The mathematical modelling of competing populations in a habitat has become quite rigorous after the work of Lotka and Volterra. It is only during the last few decades that the environmental and ecological effects have been considered on the evolutionary processes of interacting species. These effects have been taken into account by identifying species migration with dispersive and convective processes which might have continuously varying properties due to environmental as well as ecological gradients in the habitat, and may depend upon densities as well as space co-ordinates of the species, [1, 2, 5, 9, 12, 13, 14, 18, 19, 20, 21]. In particular Kapur [13] has shown that, for a general class of competition models, diffusive instability cannot arise. It is known that the opportunities for migration and habitat diversification provided by the spatial changes in environment make coexistence of species possible which could not otherwise survive. It has been shown that an unstable equilibrium

may become stable with dispersion under certain conditions in a homogeneous habitat [9].

It may, however, be noted that the habitats in general, are heterogeneous due to variety of factors such as geographical, climatic, ecological etc.. If the habitat is heterogeneous and favorable, different combinations of species are likely to be favored in some regions and maintained elsewhere principally by dispersal from more favored regions, and this process enhances the overall species richness. But opposite would be the case if the habitat becomes unfavorable to the species due to climatic changes, resource depletion such in a forest habitat which might have been degraded due to industrialization leading to patchiness.

It may be noted here that one of the methods for study the stability of interacting species model with space dependent properties is to divide the habitat in a number of patches with interaction and diffusion for each species is different but constant in each patch [3, 4, 8, 19]. The effect of patchiness on the stability of interacting population can also studied by using the same method [19]. Freedman et al., [4] studied a single species diffusion model by assuming that the habitat consists of two patches and shown that the steady-state solution is monotonically increasing and linear asymptotically stable under both reservoir and no-flux boundary conditions. Later they [3, 8] discussed the single species diffusion model in multi-patch environment and also studied the global stability for the system. In the above studies the effect of patchiness on two interacting populations has not been investigated.

Keeping the above in view, in this chapter, we study the coexistence of two competing species with logistic type growths and diffusion in both homogeneous and the two-patch habitats in the similar manner as in case of prey-predator system already studied in chapter-4. This chapter is organized as follows, in section 6.2, the complete model of two competing species in a two-patch habitat is written. In section 6.3, we study the model in a homogeneous habitat without and with diffusion and compare the stability behavior of both the system. In section 6.4, we study our main model (described in section 6.2) in a two-patch habitat for both uniform and non-uniform steady state cases under both

reservoir and no-flux boundary conditions. In the last section 6.5, we give some numerical solutions of steady state solutions with reservoir boundary conditions.

6.2 Mathematical Model

We consider a general model for two competing and diffusing species in a two-patchy habitat. Let $x_i(s,t)$ and $y_i(s,t)$ be the densities of two competing species in the i-th patch, for $i = 1, 2$. The system is then governed by the following autonomous partial differential equations:

$$\frac{\partial x_i(s,t)}{\partial t} = x_i(s,t)\mathbf{g}_i\left(x_i(s,t)\right) - y_i(s,t)\mathbf{p}_i\left(x_i(s,t)\right) + D_{1i}\frac{\partial^2 x_i(s,t)}{\partial s^2} \tag{6.1}$$

$$\frac{\partial y_i(s,t)}{\partial t} = y_i(s,t)\mathbf{f}_i\left(y_i(s,t)\right) - x_i(s,t)\mathbf{q}_i\left(y_i(s,t)\right) + D_{2i}\frac{\partial^2 y_i(s,t)}{\partial s^2} \tag{6.2}$$

$$0 \le s \le L_2 \qquad i = 1, 2$$

where the i-th patch is assumed to lie along the spatial length $L_{i-1} \le s \le L_i$ $(L_0 = 0)$, $\mathbf{g}_i(x_i)$ and $\mathbf{f}_i(y_i)$ are the respective specific growth rates, $\mathbf{p}_i(x_i)$, $\mathbf{q}_i(y_i)$ are interaction rates of $x_i(s,t)$ and $y_i(s,t)$, and D_{1i} and D_{2i} are the diffusion coefficient of x_i and y_i in the i-th patch respectively.

We assume the following assumption for $\mathbf{g}_i(x_i)$, $\mathbf{f}_i(y_i)$, $\mathbf{p}_i(x_i)$ and $\mathbf{q}_i(y_i)$

H_1: $\mathbf{g}_i(x_i)$, $\mathbf{f}_i(y_i)$, $\mathbf{p}_i(x_i)$, $\mathbf{q}_i(y_i) \in \mathrm{C}^2[0,\infty)$

$\mathbf{g}_i(0) > 0, \mathbf{f}_i(0) > 0, \mathbf{p}_i(0) = 0, \mathbf{q}_i(0) = 0$

For $x_i > 0$, $\mathbf{g}_i'(x_i) \le 0$, $\mathbf{p}_i'(x_i) > 0$

For $y_i > 0$, $\mathbf{f}_i'(y_i) \le 0$, $\mathbf{q}_i'(y_i) > 0$

When the first and second species have the carrying capacities K_i, M_i respectively in the i-th patch, then

H_2: $\quad \mathrm{g}_i(K_i) = 0, \mathrm{f}_i(M_i) = 0, \quad i = 1, 2.$

We also assume that,

H_3: $\quad \exists\ x_i^* > 0,\ y_i^* > 0$ such that

$$x_i^* \mathrm{g}_i(x_i^*) - y_i^* \mathrm{p}_i(x_i^*) = 0 \tag{6.3}$$

$$y_i^* \mathrm{f}_i(y_i^*) - x_i^* \mathrm{q}_i(y_i^*) = 0 \tag{6.4}$$

There are only two possibility of existence of positive equilibria $(x_i^*,\ y_i^*)$ (see also Fig.6.1 and Fig.6.2 in next section), either

$$\text{(i) } K_i > \frac{\mathrm{f}_i(0)}{\mathrm{q}_i'(0)},\quad M_i > \frac{\mathrm{g}_i(0)}{\mathrm{p}_i'(0)} \text{ or (ii) } K_i < \frac{\mathrm{f}_i(0)}{\mathrm{q}_i'(0)},\quad M_i < \frac{\mathrm{g}_i(0)}{\mathrm{p}_i'(0)}$$

Since from (6.3), we have, $x_i^* \mathrm{g}_i(x_i^*) = y_i^* \mathrm{p}_i(x_i^*)$, this implies that $\mathrm{g}_i(x_i^*) \geq 0 = \mathrm{g}_i(K_i)$ and again since from assumption H_1, $\mathrm{g}_i'(x_i) \leq 0$, for all $x_i \geq 0$. Hence $x_i^* \leq K_i$. Similarly from (6.4) and H_1, we get $y_i^* \leq M_i$.

We also assume the continuity and flux matching conditions at the interface $s = L_1$. The continuity conditions at the interface $s = L_1$ for this system are,

$$x_1(L_1, t) = x_2(L_1, t) \text{ and } y_1(L_1, t) = y_2(L_1, t) \tag{6.5}$$

and the continuous flux matching conditions at the interface $s = L_1$ for $x_i(s,t)$ and $y_i(s,t)$ are written as,

$$D_{11} \frac{\partial x_1(L_1, t)}{\partial s} = D_{12} \frac{\partial x_2(L_1, t)}{\partial s} \tag{6.6}$$

$$D_{21} \frac{\partial \psi_1(L_1, t)}{\partial s} = D_{22} \frac{\partial \psi_2(L_1, t)}{\partial s} \tag{6.7}$$

The model is studied under two set of boundary conditions i.e. reservoir and no-flux. In the case of reservoir boundary conditions, we take

$$x_1(0,t) = x_1^* \ , \ x_2(L_2,t) = x_2^*, \ \text{and} \ y_1(0,t) = y_1^* \ , \ y_2(L_2,t) = y_2^* \tag{6.8}$$

In the case of no-flux boundary conditions , we have

$$\frac{\partial x_1(0,t)}{\partial s} = 0 = \frac{\partial x_2(L_2,t)}{\partial s} \ \text{and} \ \frac{\partial y_1(0,t)}{\partial s} = 0 = \frac{\partial y_2(L_2,t)}{\partial s} \tag{6.9}$$

Finally the model is completed by assuming some positive initial distribution, that is,

$$x_i(s,0) = \chi_i(s) > 0, \ L_{i-1} < s < L_i, \tag{6.10}$$

$$y_i(s,0) = \delta_i(s) > 0, \ L_{i-1} < s < L_i. \tag{6.11}$$

We first study the existence and stability behavior of the system (6.1) and (6.2) in a homogeneous habitat without patchiness, the effect of patchiness will be investigated later.

6.3 Analysis of the Model in a Homogeneous Habitat

6.3.1 Model without Diffusion

In this case $x_i = x$, $y_i = y$, $\mathrm{g}_i(x_i) = \mathrm{g}(x)$, $\mathrm{f}_i(y_i) = \mathrm{f}(y)$, $\mathrm{p}_i(x_i) = \mathrm{p}(x)$, $i = 1,2$. Thus the system (6.1) and (6.2) reduces to the following form:

$$\frac{dx}{dt} = x\mathrm{g}(x) - y\mathrm{p}(x) \tag{6.12}$$

$$\frac{dy}{dt} = y\mathrm{f}(y) - x\mathrm{q}(y) \tag{6.13}$$

The functions $\mathbf{g}(x)$, $\mathbf{f}(y)$ and $\mathbf{p}(x)$ satisfy the same type of assumption as mentioned in $\mathbf{H_1}$ and $\mathbf{H_2}$. And the assumption $\mathbf{H_3}$ can be written as, $\exists\ x^* > 0$ and $y^* > 0$ such that,

$$x^*\mathbf{g}(x^*) - y^*\mathbf{p}(x^*) = 0 \tag{6.14}$$

$$y^*\mathbf{f}(y^*) - x^*\mathbf{q}(y^*) = 0 \tag{6.15}$$

From equations (6.14) and (6.15) it follows that there are four equilibria, namely (i) $E_0 = [0, 0]$, (ii) $E_K = [K, 0]$, (iii) $E_M = [0, M]$ and (iv) $E^* = [x^*, y^*]$. The existence of E^*, the interior equilibrium can be ensure by (see Fig.6.1 and Fig.6.2), either

$$\text{Case (i) } K > \frac{\mathbf{f}(0)}{\mathbf{q}'(0)},\quad M > \frac{\mathbf{g}(0)}{\mathbf{p}'(0)} \text{ or Case (ii) } K < \frac{\mathbf{f}(0)}{\mathbf{q}'(0)},\quad M < \frac{\mathbf{g}(0)}{\mathbf{p}'(0)}$$

Note: Now we note from the two isoclines given by (6.12) and (6.13) i.e.,

$$y = \frac{x\mathbf{g}(x)}{\mathbf{p}(x)} \quad \text{and} \quad x = \frac{y\mathbf{f}(y)}{\mathbf{q}(y)},$$

that the gradients at (x^*, y^*) are respectively, given as follows

$$\left(\frac{dy}{dx}\right)_{(x^*,y^*)} = \frac{H_1^*}{\mathbf{p}(x^*)} \quad \text{and} \quad \left(\frac{dy}{dx}\right)_{(x^*,y^*)} = \frac{\mathbf{q}(y^*)}{H_2^*}.$$

Now from Fig. 6.1, we have

$$-\frac{\mathbf{q}(y^*)}{H_2^*} > -\frac{H_1^*}{\mathbf{p}(x^*)}, \text{ i.e. } \frac{\mathbf{q}(y^*)}{-H_2^*} > \frac{-H_1^*}{\mathbf{p}(x^*)}.$$

Multiplying both side by $-H_2^*\mathbf{p}(x^*)$, we get $\mathbf{p}(x^*)\mathbf{q}(y^*) > H_1^*H_2^*$, provived $H_1^* < 0$ and $H_2^* < 0$. But from Fig.6.2, by similar manner, we get

$$-\frac{\mathbf{q}(y^*)}{H_2^*} < -\frac{H_1^*}{\mathbf{p}(x^*)} \Rightarrow \mathbf{p}(x^*)\mathbf{q}(y^*) < H_1^*H_2^*$$

Therefore the conditions $\mathbf{p}(x^*)\mathbf{q}(y^*) > H_1^*H_2^*$ corresponds to case (i) [Fig.6.1] above and other condition corresponds to case (ii) [Fig.6.2]. ∎

Now, the variational matrix, in the general case, is given by

$$[M] = \begin{bmatrix} \mathbf{g}(x) + x\mathbf{g}'(x) - y\mathbf{p}'(x) & -\mathbf{p}(x) \\ -\mathbf{q}(y) & \mathbf{f}(y) + y\mathbf{f}'(y) - x\mathbf{q}'(y) \end{bmatrix}. \tag{6.16}$$

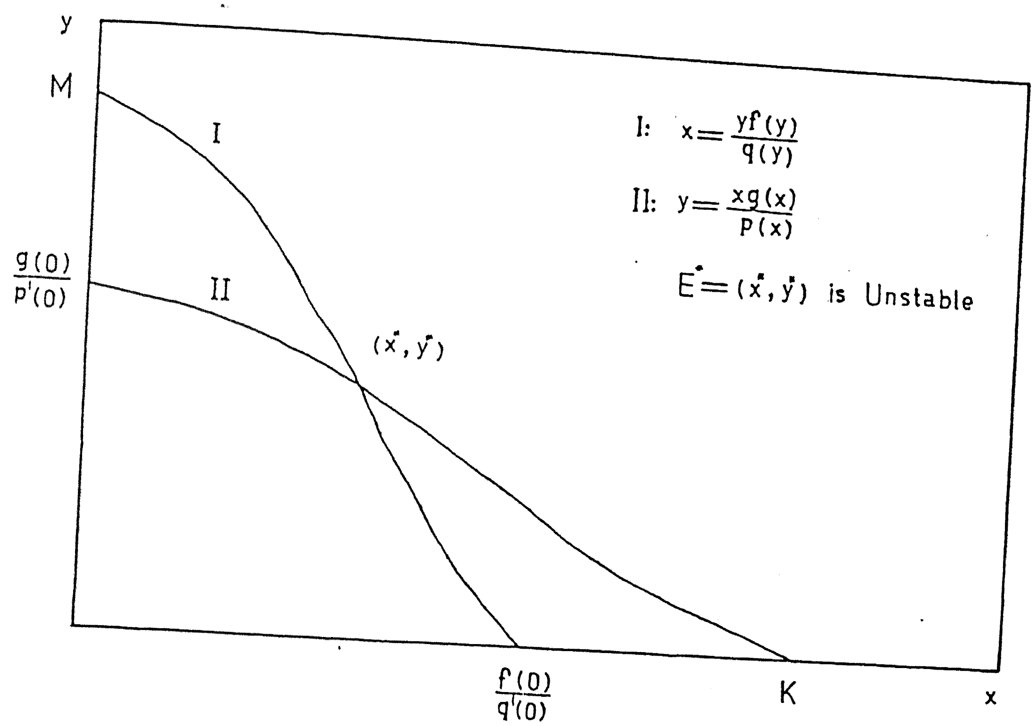


Figure 6.1: Existence of E^*, i.e. (x^*, y^*) [for case (i)]

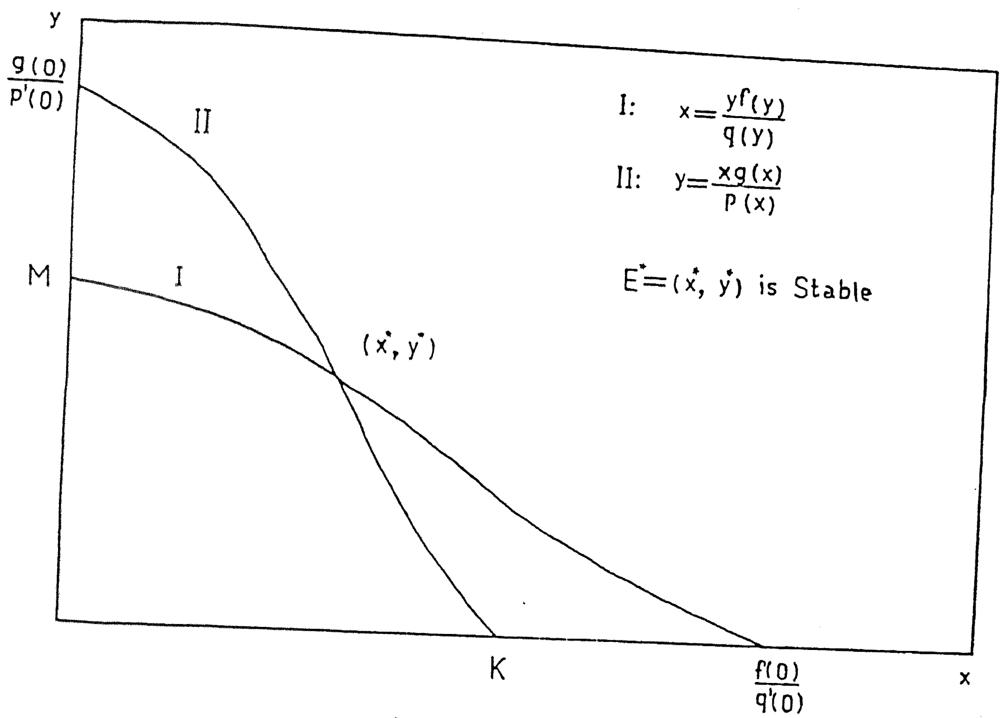


Figure 6.2: Existence of E^*, i.e. (x^*, y^*) [for case (ii)]

Now calculating the variational matrix from (6.16) for each equilibria and noting the hypotheses $\mathbf{H_1} \rightarrow \mathbf{H_3}$ and the standard stability theory of ordinary differential equations, we note the following obvious remarks:

The equilibrium point E_0 is always unstable. The equilibrium point E_K is a stable or saddle point according as $\mathrm{f}(0) - K\mathrm{q}'(0)$ is negative or positive. Similarly the E_M is a stable or saddle point according as $\mathrm{g}(0) - M\mathrm{p}'(0)$ is negative or positive. In general, there is no obvious remark to be made about the stability of the most interesting non-zero equilibria E^*, if it exists.

Therefore, our aim of this section is to obtain local stability and as well as global stability conditions for E^*.

We now state main results of this section in the forms of Theorems 6.3.1, and 6.3.2 and Lemma 6.3.1.

Theorem 6.3.1 *The equilibrium E^* is locally asymptotically stable, if the following conditions are satisfied,*

$$H_1^* < 0, \quad H_2^* < 0, \tag{6.17}$$

and

$$\mathrm{p}(x^*)\mathrm{q}(y^*) < H_1^* H_2^* \tag{6.18}$$

where

$$H_1^* = x^*\mathrm{g}'(x^*) + \mathrm{g}(x^*) - \frac{x^*\mathrm{g}(x^*)}{\mathrm{p}(x^*)}\mathrm{p}'(x^*) \quad \text{and} \quad H_2^* = y^*\mathrm{f}'(y^*) + \mathrm{f}(y^*) - \frac{y^*\mathrm{f}(y^*)}{\mathrm{q}(y^*)}\mathrm{q}'(y^*)$$

∎

Proof: By considering the following positive definite function

$$V(x, y) = \frac{1}{2}[(x - x^*)^2 + (y - y^*)^2]$$

the theorem can be proved.[see proof of theorem 4.3.1].

As discussed before it may noted that the condition (6.18) satisfied only in case (ii), i.e. corresponds to Fig.6.2. Hence E^* is locally stable in case (ii).

The final result of this section, Theorem 6.3.2 gives us the criteria for E^* to be globally asymptotically stable. First we prove a lemma which establishes a region of attraction of the system.

Lemma 6.3.1 *The region of attraction for all solutions initiating in the positive quadrant is*

$$\mathcal{A} = \{(x, y) : 0 \leq x \leq K, 0 \leq y \leq M\}$$

Proof: From (6.12) and (6.13) and hypotheses (H_1) to (H_3), we get,

$$\begin{aligned} \dot{x}(t) \leq x(t)\mathrm{g}(x(t)) &\leq \mathrm{g}(0)x(t)[1 - x(t)/K], \text{ and} \\ \dot{y}(t) \leq y(t)\mathrm{f}(y(t)) &\leq \mathrm{f}(0)y(t)[1 - y(t)/M], \end{aligned}$$

then, as $t \to \infty$,

$$\begin{aligned} &\text{for } x(0) < K, \;\; \mathit{lim\ sup}\ x(t) \leq K, \text{ and for } \;\; x(0) > K, \;\; \mathit{lim\ sup}\ x(t) \to K, \\ &\text{for } y(0) < M, \;\; \mathit{lim\ sup}\ y(t) \leq M, \text{ and for } \;\; y(0) > M, \;\; \mathit{lim\ sup}\ y(t) \to M. \end{aligned}$$

Therefore, we note that solutions initiating on $\delta\mathcal{A} \cap \mathit{int}\ \mathcal{R}^+$ enter into $\mathit{int}\ \mathcal{A}$. Hence $\mathcal{A}$ is the region of attraction of the given system. ∎

Theorem 6.3.2 *Let the conditions*

$$(x - x^*)[x\mathrm{g}(x) - y^*\mathrm{p}(x)] < 0, \quad \forall\, x \neq x^*,\ y \neq y^* \tag{6.19}$$

$$(y - y^*)[y\mathrm{f}(y) - x^*\mathrm{q}(y)] < 0, \quad \forall\, x \neq x^*,\ y \neq y^* \tag{6.20}$$

$$\left[\frac{\mathrm{p}(x)}{x}+\frac{\mathrm{q}(y)}{y}\right]^2 < \frac{4}{xy}\left[\frac{x\mathrm{g}(x)-y^*\mathrm{p}(x)}{x-x^*}\right]\left[\frac{y\mathrm{f}(y)-x^*\mathrm{q}(y)}{y-y^*}\right]$$
$$\Rightarrow \quad \mathrm{p}(x)\mathrm{q}(y) < \left[\frac{x\mathrm{g}(x)-y^*\mathrm{p}(x)}{x-x^*}\right]\left[\frac{y\mathrm{f}(y)-x^*\mathrm{q}(y)}{y-y^*}\right] \tag{6.21}$$

hold. Then E^* (in Fig.6.2) which is locally stable is also globally asymptotically stable in $\mathcal{A}$. ∎

Proof: By considering the following positive definite function

$$V(x,y) = \left(x - x^* - x^* ln\frac{x}{x^*}\right) + \left(y - y^* - y^* ln\frac{y}{y^*}\right)$$

the theorem can be proved.[see proof of theorem 4.3.3].

Remark: If we linearize (6.19) and (6.20), around the equilibrium point E^*, we get $H_1^* < 0$ and $H_2^* < 0$.

In the following example we show that the conditions for the local and the global stability are feasible.

Example: We take,

$$\mathrm{g}(x) = r\left(1-\frac{x}{K}\right), \quad \mathrm{f}(y) = s\left(1-\frac{y}{M}\right), \quad \mathrm{p}(x) = \alpha_1 x \ \text{ and } \ \mathrm{q}(y) = \alpha_2 y$$

Then the the equilibrium point $E^*(x^*, y^*)$ is given by

$$x^* = \frac{sK(r-\alpha_1 M)}{rs - \alpha_1\alpha_2 KM}, \quad y^* = \frac{rM(s-\alpha_2 K)}{rs-\alpha_1\alpha_2 KM} \tag{6.22}$$

From (6.22) it is clear that positive equilibria exists under two set of conditions, namely

Case 1: $r < \alpha_1 M$, $s < \alpha_2 K$ and $rs < \alpha_1\alpha_2 KM$

Case 2: $r > \alpha_1 M$, $s > \alpha_2 K$ and $rs > \alpha_1\alpha_2 KM$

The nature of x^* and y^* with respect to various parameters can be calculated from (6.22). It is shown in the following table,

Table 6.3: Effects of various parameters on x^* and y^*

x(i)	$r\uparrow$	$x_i^*\downarrow$	$y_i^*\uparrow$	Case 1
		$x_i^*\uparrow$	$y_i^*\downarrow$	Case 2
(ii)	$s\uparrow$	$x_i^*\uparrow$	$y_i^*\downarrow$	Case 1
		$x_i^*\downarrow$	$y_i^*\uparrow$	Case 2
(iii)	$K\uparrow$	$x_i^*\downarrow$	$y_i^*\uparrow$	Case 1
		$x_i^*\uparrow$	$y_i^*\downarrow$	Case 2
(iv)	$M\uparrow$	$x_i^*\uparrow$	$y_i^*\downarrow$	Case 1
		$x_i^*\downarrow$	$y_i^*\uparrow$	Case 2
(v)	$\alpha_1\uparrow$	$x_i^*\uparrow$	$y_i^*\downarrow$	Case 1
		$x_i^*\downarrow$	$y_i^*\uparrow$	Case 2
(vi)	$\alpha_2\uparrow$	$x_i^*\downarrow$	$y_i^*\uparrow$	Case 1
		$x_i^*\uparrow$	$y_i^*\downarrow$	Case 2

Now we note that , $H_1^* = -rx^*/K < 0$, $H_2^* = -sy^*/M < 0$

$\dfrac{[x\mathrm{g}(x) - y^*\mathrm{p}(x)]}{x - x^*} == -\dfrac{rx}{K} < 0$ and $\dfrac{[y\mathrm{f}(y) - x^*\mathrm{q}(y)]}{y - y^*} == -\dfrac{sy}{M} < 0 \ \forall x \neq x^*, \ y \neq y^*.$

Therefore the condition (6.19) and (6.20) are automatically satisfied. Further both the local and global stability condition (6.18) and (6.21) becomes,

$$\alpha_1\alpha_2 < \frac{rs}{KM},$$

which is automatically satisfied in Case 2. Hence E^* is locally as well as globally asymptotically stable in Case 2.

6.3.2 Model with Diffusion

Now, we wish to consider the model (6.12) and (6.13) with diffusion and analyze the uniform equilibrium E^* under both reservoir and no-flux boundary conditions. The model (6.12) and (6.13) in this case can be written as,

$$\frac{\partial x}{\partial t} = x\mathrm{g}(x) - y\mathrm{p}(x) + D_1\frac{\partial^2 x}{\partial s^2} \tag{6.23}$$

$$\frac{\partial y}{\partial t} = y\mathrm{f}(y) - x\mathrm{q}(y)] + D_2\frac{\partial^2 y}{\partial s^2} \tag{6.24}$$

$$0 \leq s \leq L$$

where $D_i \geq 0$ are diffusion coefficients. The reservoir and no-flux boundary conditions are respectively,

$$x(0,t) = x^* = x(L,t) \text{ and } y(0,t) = y^* = y(L,t), \tag{6.25}$$

$$\frac{\partial x(0,t)}{\partial s} = 0 = \frac{\partial x(L,t)}{\partial s} \text{ and } \frac{\partial y(0,t)}{\partial s} = 0 = \frac{\partial y(L,t)}{\partial s}. \tag{6.26}$$

Now if we take the following positive definite function

$$W(x,y) = \int_0^L V(x,y)ds,$$

around the equilibrium point E^*, then using similar arguments as in section 3.1, we get the following theorems for local and global stability of the system.

Theorem 6.3.3 *The equilibrium E^* is locally asymptotically stable, if the conditions (6.17) and (6.18) are satisfied.*

Moreover by using Poincare's inequality, it is pointed out that even if (6.18) does not hold true, this uniform equilibrium may become stable with diffusion under a condition as given in the following theorem.

Theorem 6.3.4 *The equilibrium E^* is locally asymptotically stable, if the condition (6.17), along with*

$$\mathrm{p}(x^*)\mathrm{q}(y^*) < \left(H_1^* - D_1\frac{\pi^2}{L^2}\right)\left(H_2^* - D_2\frac{\pi^2}{L^2}\right) \tag{6.27}$$

are satisfied. ∎

Theorem 6.3.5 *If the conditions (6.19)-(6.21) are satisfied. Then E^* is globally asymptotically stable in $\mathcal{A}$.*

Thus the uniform equilibrium E^* (in Fig.6.2) of the system is locally as well as globally asymptotically stable under the same set of conditions, as in the previous case. Further by Theorem 6.3.4, an equilibrium which is unstable without diffusion can become stable with diffusion.

6.4 Analysis of the Model with Diffusion in a Two-Patch Habitat

In the first subsection we study the model (6.1)- (6.11), in the case of uniform equilibrium state. In the next section we study the non-uniform case.

6.4.1 The Uniform Equilibrium State under Both Sets of Boundary Conditions

The aim of this section is to show that uniform steady-state is globally asymptotically stable. In this case, it is clear that, under both sets of boundary conditions, there is a uniform steady-state, $x(s,t) \equiv K^*$, $0 \leq s \leq L_2$, $t \geq 0$, $y(s,t) \equiv M^*$, $0 \leq s \leq L_2$, $t \geq 0$, (i=1,2) where K^* and M^* are the common uniform equilibrium point of first species and second species respectively in the two patches. Let $x_1^* = x_2^* = K^*$ and $y_1^* = y_2^* = M^*$. By using similar arguments as in section 3.1, the following theorems for stability can be proved for the system (6.1) $\rightarrow$ (6.7) with (6.8) or (6.9).

Theorem 6.4.1 *The unique uniform steady state solutions (K^*, M^*) is locally asymptotically stable, if $H_j^{i*} < 0$, for $i, j = 1, 2$, and the following conditions are satisfied,*

$$\mathrm{p}_i(K^*)\mathrm{q}_i(M^*) < H_1^{i*} H_2^{i*} \quad i = 1, 2 \tag{6.28}$$

where

$$H_1^{i*} = K^*\mathrm{g}_i'(K^*)+\mathrm{g}_i(K^*)-\frac{K^*\mathrm{g}_i(K^*)}{\mathrm{p}_i(K^*)}\mathrm{p}_i'(K^*)\,,\; H_2^{i*} = M^*\mathrm{f}_i'(M^*)+\mathrm{f}_i(M^*)-\frac{M^*\mathrm{f}_i(M^*)}{\mathrm{q}_i(M^*)}\mathrm{q}_i'(M^*)$$

∎

Similarly as in Theorem 6.3.4, the above uniform steady state is locally asymptotically stable under less stringent conditions as the following theorem,

Theorem 6.4.2 *The unique uniform steady state solutions (K^*, M^*) is locally asymptotically stable, if $H_j^{i*} - D_{ji}\pi^2/(L_i - L_{i-1})^2 < 0$, for $i, j = 1, 2$, and the following conditions*

$$\mathrm{p}_i(K^*)\mathrm{q}_i(M^*) < \left(H_1^{i*} - D_{1i}\frac{\pi^2}{(L_i - L_{i-1})^2}\right)\left(H_2^{i*} - D_{2i}\frac{\pi^2}{(L_i - L_{i-1})^2}\right), \quad i = 1, 2 \qquad (6.29)$$

are satisfied.

∎

We now state the global stability of the uniform steady state,

Theorem 6.4.3 *The uniform steady-state solutions (K^*, M^*) is globally asymptotically stable, if the following conditions are satisfied,*

$$(x_i - K^*)[x_i\mathrm{g}_i(x_i) - M^*\mathrm{p}_i(x_i)] < 0, \quad \forall\; x_i \neq x^*, \qquad (6.30)$$

$$(y_i - M^*)[y_i\mathrm{f}_i(y_i) - K^*\mathrm{q}_i(y_i)] < 0, \quad \forall\; y_i \neq M^*, \qquad (6.31)$$

$$\mathrm{p}_i(x_i)\mathrm{q}_i(y_i) < \left[\frac{x_i\mathrm{g}(x_i) - M^*\mathrm{p}_i(x_i)}{x_i - K^*}\right]\left[\frac{y_i\mathrm{f}_i(y_i) - K^*\mathrm{q}_i(y_i)}{y_i - M^*}\right] \qquad (6.32)$$

Proof: Let V(x,y) be the positive definite function about $x = K^*$, $y = M^*$, given by

$$\begin{aligned} V(t) = V(x,y) &= \sum_1^2 \int_{L_{i-1}}^{L_i} \left(x_i - K^* - K^*\ln\{\frac{x_i}{K^*}\}\right) ds \\ &+ \sum_1^2 \int_{L_{i-1}}^{L_i} \left(y_i - M^* - M^*\ln\{\frac{y_i}{M^*}\}\right) ds \end{aligned}$$

Differentiating with respect to t, and using (6.1) and (6.2) we get,

$$\begin{aligned}
\dot{V}(t) &= \sum_1^2 \int_{L_{i-1}}^{L_i} \left(\frac{x_i - K^*}{x_i}\right) \frac{\partial x_i}{\partial t} ds + \sum_1^2 \int_{L_{i-1}}^{L_i} \left(\frac{y_i - M^*}{y_i}\right) \frac{\partial y_i}{\partial t} ds \\
&= \sum_1^2 \int_{L_{i-1}}^{L_i} \left(\frac{x_i - K^*}{x_i}\right) [x_i \mathrm{g}_i(x_i) - y_i \mathrm{p}_i(x_i)]\, ds \\
&+ \sum_1^2 \int_{L_{i-1}}^{L_i} D_{1i} \left(\frac{x_i - K^*}{x_i}\right) \frac{\partial^2 x_i}{\partial s^2} ds + \sum_1^2 \int_{L_{i-1}}^{L_i} \left(\frac{y_i - M^*}{y_i}\right) [y_i \mathrm{f}_i(y_i) - x_i \mathrm{q}_i(y_i)]\, ds \\
&+ \sum_1^2 \int_{L_{i-1}}^{L_i} D_{2i} \left(\frac{y_i - M^*}{y_i}\right) \frac{\partial^2 y_i}{\partial s^2} ds
\end{aligned}$$

Now by assumption (6.33), first integral of the right hand side is negative, $\forall\ x_i$, except $x_i = K^*$, $i = 1, 2$. Similarly by (6.34) the third integral of right hand side is negative, $\forall\ y_i$, except $y_i = M^*$, $i = 1, 2$.

Now consider the integral,

$$I_1 = \sum_1^2 \int_{L_{i-1}}^{L_i} D_{1i} \left(\frac{x_i - K^*}{x_i}\right) \frac{\partial^2 x_i}{\partial s^2} ds$$

Under both set of boundary conditions,

$$[x_1(0,t) - K^*] \frac{\partial x_1(0,t)}{\partial s} = [x_2(L_2,t) - K^*] \frac{\partial x_2(L_2,t)}{\partial s} = 0$$

$$I_1 = -\sum_1^2 \int_{L_{i-1}}^{L_i} D_{1i} \frac{K^*}{x_i^2} \left(\frac{\partial x_1}{\partial s}\right)^2 ds < 0$$

Similarly,

$$I_2 = \sum_1^2 \int_{L_{i-1}}^{L_i} D_{2i} \left(\frac{y_i - M^*}{y_i}\right) \frac{\partial^2 y_i}{\partial s^2} ds < 0$$

Hence $V(x, y) < 0$, and $\dot{V}(K^*, M^*) = 0$. Therefore $\dot{V}(x, y)$ is negative definite over $x > 0$, $y > 0$ with respect to $x = K^*$, $y = M^*$, proving the theorem. ∎

6.4.2 The Non-Uniform Equilibrium State

We assume that the unsteady state solutions of the model (6.1) to (6.11) exists. [see [18] (Theorem 1, page 111 and Theorem 3, page 123)].

Our aim here, therefore, is to show that there exists a positive, monotonic, continuous steady state solution for the each of the species separately, under continuous flux matching at the interface of these patches, in cases of both reservoir and no-flux boundary conditions and derive the conditions for asymptotic stability for both linear and non-linear models.

There are four possible cases:

(1) $x_2^* > x_1^*$ and $y_2^* > y_1^*$
(2) $x_2^* > x_1^*$ and $y_2^* < y_1^*$
(3) $x_2^* < x_1^*$ and $y_2^* < y_1^*$
(4) $x_2^* < x_1^*$ and $y_2^* > y_1^*$

Without loss of generality, (3) can be reduced to (1) and (4) can be reduced to (2). Therefore we consider the case (1) and (2) separately under two set of boundary conditions.

We assume the following conditions on x_i and y_i for $i = 1, 2$.

$$(x_i - x_i^*)[x_i \mathrm{g}_i(x_i) - y_i \mathrm{p}_i(x_i)] < 0, \ \forall x_i \neq x_i^* \text{ and } min.\{y_1^*, y_2^*\} \leq y_i \leq max.\{y_1^*, y_2^*\} \quad (6.33)$$

$$(y_i - y_i^*)[y_i \mathrm{f}_i(y_i) - x_i \mathrm{q}_i(y_i)] < 0, \ \ \forall y_i \neq y_i^* \text{ and } min.\{x_1^*, x_2^*\} \leq x_i \leq max.\{x_1^*, x_2^*\} \quad (6.34)$$

The alalysis in the remaining part of this chapter is valid under these two conditions, (6.33) and (6.34).

6.4.3 The Model under Reservoir Boundary Conditions: When $x_2^* > x_1^*$ and $y_2^* > y_1^*$.

We first consider the steady-state problem and show that there exists a non-uniform positive monotonic solutions $u_i(s)$, $v_i(s)$ under reservoir boundary conditions and with continuous flux at the interface.

The steady-state system takes the form

$$D_{1i}\frac{d^2 u_i(s)}{ds^2} + u_i \mathrm{g}_i(u_i) - v_i \mathrm{p}_i(u_i) = 0 \quad (6.35)$$

$$D_{2i}\frac{d^2v_i(s)}{ds^2} + v_i\mathrm{f}_i(v_i) - u_i\mathrm{q}_i(v_i) = 0 \tag{6.36}$$

The reservoir boundary conditions are

$$u_1(0) = x_1^*, u_2(L_2) = x_2^* \tag{6.37}$$

$$v_1(0) = y_1^*, v_2(L_2) = y_2^* \tag{6.38}$$

The continuous solutions and flux matching conditions at the interface are

$$u_1(L_1) = u_2(L_1); v_1(L_1) = v_2(L_1) \tag{6.39}$$

$$D_{11}\frac{du_1(L_1)}{ds} = D_{12}\frac{du_2(L_1)}{ds} \tag{6.40}$$

$$D_{21}\frac{dv_1(L_1)}{ds} = D_{22}\frac{dv_2(L_1)}{ds} \tag{6.41}$$

Let $p_1(s,\alpha_1)$ and $q_1(s,\beta_1), 0 \leq s \leq L_1$ be the unique solutions of (6.35) and (6.36) respectively, for i=1, such that

$$\frac{\partial p_1(0,\alpha_1)}{\partial s} = \alpha_1, \quad p_1(0,\alpha_1) = x_1^* \tag{6.42}$$

$$\frac{\partial q_1(0,\beta_1)}{\partial s} = \beta_1, \quad q_1(0,\beta_1) = y_1^* \tag{6.43}$$

Let $p_2(s,\alpha_2)$ and $q_2(s,\beta_2), L_1 \leq s \leq L_2$ be the unique solutions of (6.35) and (6.36) respectively, for i=2, such that

$$\frac{\partial p_2(L_2,\alpha_2)}{\partial s} = \alpha_2, \quad p_2(L_2,\alpha_2) = x_2^* \tag{6.44}$$

$$\frac{\partial q_2(L_2,\beta_2)}{\partial s} = \beta_2, \quad q_2(L_2,\beta_2) = y_2^* \tag{6.45}$$

The existence of the monotonic solutions follows, if we can show that there exist $\alpha_1, \alpha_2, \beta_1$ and β_2 such that

$$p_1(L_1,\alpha_1) = p_2(L_1,\alpha_2)\ ,\ q_1(L_1,\beta_1) = q_2(L_1,\beta_2) \tag{6.46}$$

$$D_{11}\frac{\partial p_1(L_1,\alpha_1)}{\partial s} = D_{12}\frac{\partial p_2(L_1,\alpha_2)}{\partial s}\ ,\ D_{21}\frac{\partial q_1(L_1,\beta_1)}{\partial s} = D_{12}\frac{\partial q_2(L_1,\beta_2)}{\partial s} \tag{6.47}$$

From (6.35), multiplying both side by $2du_i/ds$ and integrating w.r.to s from 0 if i=1 and from L_2 if i=2 , we get,

$$\left[\frac{du_i}{ds}\right]^2 = \alpha_i^2 - \frac{2}{D_{1i}}\int_{x_i^*}^{u_i(s)} [u_i \mathrm{g}_i(u_i) - v_i \mathrm{p}_i(u_i)]du_i(s) \tag{6.48}$$

Similarly from (6.36), we have,

$$\left[\frac{dv_i}{ds}\right]^2 = \beta_i^2 - \frac{2}{D_{2i}}\int_{y_i^*}^{v_i(s)} [v_i \mathrm{f}_i(v_i) - u_i \mathrm{q}_i(v_i)]dv_i(s) \tag{6.49}$$

In order to construct our required solution we need some preliminary lemmas. We prove these lemmas are similar as in chapter-4.

Lemma 6.4.1 *If* $\alpha_1 > 0$, *then*

$$\frac{\partial p_1(s,\alpha_1)}{\partial s} > \alpha_1 \ on\ 0 < s \le L_1.$$

Proof: From (6.48), we get,

$$\left[\frac{\partial p_1(s,\alpha_1)}{\partial s}\right]^2 = \alpha_1^2 - \frac{2}{D_{11}}\int_{x_1^*}^{p_1(s,\alpha_1)} [p_1 \mathrm{g}_1(p_1) - q_1 \mathrm{p}_1(p_1)]dp_1 \tag{6.50}$$

since

$$\frac{\partial p_1(0,\alpha_1)}{\partial s} = \alpha_1 > 0\ ,\ p_1(0,\alpha_1) = x_1^*\ ,$$

Then there exists $s_1 > 0$ such that $p_1(s,\alpha_1) > x_1^*$ on $0 < s < s_1$. If not, let $s_0, 0 < s_0 \le L_1$, be the first positive value, if it exists, such that $p_1(s_0,\alpha_1) = x_1^*$. Then by the mean value theorem there exists $\bar{s}$ such that $0 < \bar{s} < s_0$ and $\partial p_1(\bar{s},\alpha_1)/\partial s = 0$; that is,

$$\alpha_1^2 = \frac{2}{D_{11}}\int_{x_1^*}^{p_1(\bar{s},\alpha_1)} [p_1 \mathrm{g}_1(p_1) - q_1 \mathrm{p}_1(p_1)]dp_1. \tag{6.51}$$

Now since $p_1(s,\alpha_1) > x_1^*$ for $0 < s \le \bar{s}$, and from (6.33), we have, $p_1\mathrm{g}_1(p_1) - q_1\mathrm{p}_1(p_1) <$ ce the right hand side of (6.51) is negative , giving a contradiction. Therefore

$p_1(s,\alpha_1) > x_1^*$ and $\partial p_1(s,\alpha_1)/\partial s > 0$. Now, noting that $(\partial p_1(s,\alpha_1)/\partial s)^2$ is an increasing function of p_1, the lemma follows.

∎

Lemma 6.4.2 *If* $0 < p_2 < x_2^*$ *and* $\alpha_2 > 0$*, then*

$$\frac{\partial p_2(s,\alpha_2)}{\partial s} > \alpha_2, \quad L_1 \leq s < L_2.$$

Proof: From (6.48), we have,

$$\left[\frac{\partial p_2(s,\alpha_2)}{\partial s}\right]^2 = \alpha_2^2 - \frac{2}{D_{12}}\int_{x_2^*}^{p_2(s,\alpha_2)}[p_2 \mathrm{g}_2(p_2) - q_2 \mathrm{p}_2(p_2)]dp_2$$

From (6.33), we have, $p_2\mathrm{g}_2(p_2) - q_2\mathrm{p}_2(p_2) > 0$. Hence $\partial p_2(s,\alpha_2)/\partial s > \alpha_2$, $L_1 \leq s < L_2$ for $0 < p_2 < x_2^*$.

∎

Similarly from (6.49) and (6.34) we have,

Lemma 6.4.3 *If* $\beta_1 > 0$ *, then*

$$\frac{\partial q_1(s,\beta_1)}{\partial s} > \beta_1 \text{ on } 0 < s \leq L_1.$$

Lemma 6.4.4 *If* $0 < q_2 < y_2^*$ *and* $\beta_2 > 0$*, then*

$$\frac{\partial q_2(s,\beta_2)}{\partial s} > \beta_2, \quad L_1 \leq s < L_2.$$

There exist four continuous functions F_{ji} (i,j=1,2), for proof see same lemma in chapter 2.

Lemma 6.4.5 *Define $F_{1i}(\alpha_i)$ by $F_{1i}(\alpha_i) = p_i(L_1, \alpha_i)$. Then there exists $\hat{\alpha}_i > 0$ such that*

$$F_{11} : [0, \hat{\alpha}_1] \to [x_1^*, x_2^*]$$

$$F_{12} : [0, \hat{\alpha}_2] \to [x_2^*, x_1^*]$$

Lemma 6.4.6 *Define $F_{2i}(\beta_i)$ by $F_{2i}(\beta_i) = q_i(L_1, \beta_i)$. Then there exists $\hat{\beta}_i > 0$ such that*

$$F_{11} : \left[0, \hat{\beta}_1\right] \to [x_1^*, x_2^*]$$

$$F_{12} : \left[0, \hat{\beta}_2\right] \to [x_2^*, x_1^*]$$

Theorem 6.4.4 *There exists a positive, continuous, monotonic solution of the steady state system (6.35) with continuous flux at L_1.*

Proof: From lemmas 6.4.1 and 6.4.2, it follows that any solution, we construct, must be monotonic. By Lemma 6.4.5, for each $0 \leq \alpha_2 \leq \hat{\alpha}_2$, we can find an α_1 such that $0 \leq \alpha_1 \leq \hat{\alpha}_1$ for which $p_1(L_1, \alpha_1) = p_2(L_1, \alpha_2)$. Hence α_1 can be solved as a function of α_2, $\alpha_1 = h(\alpha_2)$, to give a continuous solution of (6.35) with (6.37), (6.39) and (6.40).

Let

$$\mathrm{G}(\alpha_2) = D_{11}\frac{\partial p_1(L_1, h(\alpha_2))}{\partial s} - D_{12}\frac{\partial p_2(L_1, \alpha_2)}{\partial s}.$$

Clearly $\mathrm{G}(\alpha_2)$ is continuous on $0 \leq \alpha_2 \leq \hat{\alpha}_2$. Then we have

$$\mathrm{G}(0) = D_{11}\frac{\partial p_1(L_1, \hat{\alpha}_1)}{\partial s} > 0,$$

and

$$G(\hat{\alpha}_2) = -D_{12}\frac{\partial p_2(L_1,\hat{\alpha}_2)}{\partial s} < 0.$$

Therefore $\exists\ \bar{\alpha}_2,\ 0 < \bar{\alpha}_2 < \hat{\alpha}_2$, such that $G(\bar{\alpha}_2) = 0$. Hence the theorem. ∎

Similar results are also true for the second species.

Theorem 6.4.5 *There exists a continuous, monotonic solution of the system (6.36) with continuous flux at L_1.*

We now study the asymptotic stability of the steady state system (6.35) and (6.36 to (6.41).

Theorem 6.4.6 *The steady state, continuous, monotonic solutions of system (6.35) and (6.36) with continuous flux at the interface $s = L_1$ is asymptotically stable provided the following conditions are satisfied:*

(i) $\dfrac{d}{du_i}[u_i g_i(u_i)] \le 0$,

(ii) $\dfrac{d}{dv_i}[v_i f_2(v_i)] \le 0$, *and*

(iii) $[p_i(u_i) + q_i(v_i)]^2 < 4\left[\dfrac{d}{du_i}[u_i g_i(u_i)]\right]\left[\dfrac{d}{dv_i}[v_i f_i(v_i)]\right]$

for $x_1^* \le u_i \le x_2^*,\quad M_1 \le v_2 \le M_2$ *and* $i = 1, 2$.

'roof: Let the steady-state solution of system (6.35) be

$$u(s) = \begin{cases} u_1(s), & 0 \le s \le L_1 \\ u_2(s), & L_1 \le s \le L_2 \end{cases}$$

And let the steady-state solution of system (6.36) be

$$v(s) = \begin{cases} v_1(s), & 0 \le s \le L_1 \\ v_2(s), & L_1 \le s \le L_2 \end{cases}$$

Lineariazing (6.1) and (6.2) by using ,

$$x_i(s,t) = u_i(s) + n_i(s,t) \tag{6.52}$$

$$y_i(s,t) = v_i(s) + m_i(s,t) \tag{6.53}$$

We have,

$$\frac{\partial n_i(s,t)}{\partial t} = n_i\left[\mathrm{g}_i(u_i) + u_i\mathrm{g}_i'(u_i)\right] - n_i v_i \mathrm{p}_i'(u_i) - m_i\mathrm{p}_i(u_i) + D_{1i}\frac{\partial^2 n_i}{\partial s^2} \tag{6.54}$$

$$\frac{\partial m_i(s,t)}{\partial t} = m_i\left[\mathrm{f}_i(v_i) + v_i\mathrm{f}_i'(v_i)\right] - m_i u_i \mathrm{q}_i'(v_i) - n_i\mathrm{q}_i(v_i) + D_{2i}\frac{\partial^2 m_i}{\partial s^2} \tag{6.55}$$

Using (6.52) and (6.53) the corresponding initial , boundary and matching conditions can be obtained as follows

$$\begin{aligned} n_i(s,0) &= \chi_i(s) - u_i(s), \ m_i(s,0) = \delta_i(s) - v_i(s) \\ n_1(0,t) &= 0 = n_2(L_2,t) \ , \ m_1(0,t) = 0 = m_2(L_2,t) \\ n_1(L_1,t) &= n_2(L_1,t) \ , \ m_1(L_1,t) = m_2(L_1,t) \\ D_{11}\frac{\partial n_1}{\partial s}(L_1,t) &= D_{12}\frac{\partial n_2}{\partial s}(L_1,t) \\ D_{21}\frac{\partial m_1}{\partial s}(L_1,t) &= D_{22}\frac{\partial m_2}{\partial s}(L_1,t) \end{aligned} \tag{6.56}$$

Now we consider the following positive definite function,

$$V(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \frac{1}{2}\left[n_i^2 + m_i^2\right] ds$$

From which we get,

$$\dot{V}(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \left[n_i\frac{\partial n_i}{\partial t} + m_i\frac{\partial m_i}{\partial t}\right] ds$$

By using (6.54) and (6.55) , we get,

$$\begin{aligned}
\dot{V}(t) \;=\; & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2 \left[\mathrm{g}_i(u_i) + u_i \mathrm{g}_i'(u_i)\right] ds - \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2 v_i \mathrm{p}_i'(u_i) ds \\
& - \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i \mathrm{p}_i(u_i) ds - \sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} \left[\frac{\partial m_i}{\partial s}\right]^2 ds \\
& + \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2 \left[\mathrm{f}_i(v_i) + v_i \mathrm{f}_i'(v_i)\right] ds - \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2 u_i \mathrm{q}_i'(v_i) ds \\
& - \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i \mathrm{q}_i(v_i) ds - \sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} \left[\frac{\partial n_i}{\partial s}\right]^2 ds
\end{aligned}$$

Since $\mathrm{p}_i'(u_i) > 0$, $\forall x_i \geq 0$. Therefore second integral of the right hand side of above equation is negative. Similarly sixth integral is also negative. Hence $V(t)$ is negative definite if conditions (i), (ii) and (iii) are satisfies, and the theorem is proved. ∎

Theorem 6.4.7 *The steady-state ,continuous ,monotonic solutions of non-linear system (6.35) to (6.41) with continuous flux at the interface $s = L_1$ is asymptotically stable in the subregion of* $\mathbf{R}$: $\{x_1^* \leq x_i,\ u_i \leq x_2^*,\ y_1^* \leq y_i,\ v_i \leq y_2^*,\ for\ i = 1, 2\}$, *provided the following conditions are satisfied:*

(1) $$\frac{x_i \mathrm{g}_i(x_i) - u_i \mathrm{g}_i(u_i)}{x_i - u_i} \leq 0\,,$$

(2) $$\frac{y_i \mathrm{f}_i(y_i) - v_i \mathrm{f}_i(v_i)}{y_i - v_i} \leq 0\,,$$

(3) $$x_i y_i \left[\frac{u_i \mathrm{p}_i(x_i)}{x_i} + \frac{v_i \mathrm{q}_i(y_i)}{y_i}\right]^2 < 4 u_i v_i \left[\frac{x_i \mathrm{g}_i(x_i) - u_i \mathrm{g}_i(u_i)}{x_i - u_i}\right]\left[\frac{y_i \mathrm{f}_i(y_i) - v_i \mathrm{f}_i(v_i)}{y_i - v_i}\right]$$

Proof: From (6.1),(6.2),(6.52) and (6.53), we have

$$\frac{\partial n_i}{\partial t} = (u_i + n_i)\mathrm{g}_i(u_i + n_i) - u_i \mathrm{g}_i(u_i) - (v_i + m_i)\mathrm{p}_i(u_i + n_i) + v_i p_i(u_i) + D_{1i} \frac{\partial^2 n_i}{\partial s^2} \quad (6.57)$$

$$\frac{\partial m_i}{\partial t} = (v_i + m_i)\mathbf{f}_i(v_i + m_i) - v_i\mathbf{f}_i(v_i) - (u_i + n_i)\mathbf{q}_i(v_i + m_i) + u_i q_i(v_i) + D_{2i}\frac{\partial^2 m_i}{\partial s^2} \quad (6.58)$$

Now consider the positive definite function,

$$V(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \frac{1}{2}[(x_i - u_i)^2 + (y_i - v_i)^2]ds = \sum_1^2 \int_{L_{i-1}}^{L_i} \frac{1}{2}[n_i^2 + m_i^2]ds$$

From which we get,

$$\dot{V}(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} n_i \frac{\partial n_i}{\partial t} ds + \sum_1^2 \int_{L_{i-1}}^{L_i} m_i \frac{\partial m_i}{\partial t} ds$$

After using equations (6.57) and (6.58), we get

$$\begin{aligned}
\dot{V}(t) &= \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2 \left[\frac{(u_i + n_i)\mathbf{g}_i(u_i + n_i) - u_i\mathbf{g}_i(u_i)}{n_i}\right] ds \\
&- \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2 \left[v_i \left(\frac{\mathbf{p}_i(u_i + n_i) - \mathbf{p}_i(u_i)}{n_i}\right)\right] ds \\
&- \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i \mathbf{p}_i(u_i + n_i) ds + \sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} n_i \frac{\partial^2 n_i}{\partial s^2} ds \\
&+ \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2 \left[\frac{(v_i + m_i)\mathbf{f}_i(v_i + m_i) - v_i\mathbf{f}_i(v_i)}{m_i}\right] ds \\
&- \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2 \left[u_i \left(\frac{\mathbf{q}_i(v_i + m_i) - \mathbf{q}_i(v_i)}{m_i}\right)\right] ds \\
&- \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i \mathbf{q}_i(v_i + m_i) ds + \sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} m_i \frac{\partial^2 m_i}{\partial s^2} ds
\end{aligned}$$

Now,

$$\frac{\mathbf{p}_i(u_i + n_i) - \mathbf{p}_i(u_i)}{n_i} \geq 0, \quad \forall\, n_i.$$

$$\frac{\mathbf{q}_i(v_i + m_i) - \mathbf{q}_i(v_i)}{m_i} \geq 0, \quad \forall\, m_i.$$

Also by using (6.56), we get

$$\sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} n_i \frac{\partial^2 n_i}{\partial s^2} ds = -\sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial n_i}{\partial s}\right)^2 ds < 0$$

Similarly

$$\sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} m_i \frac{\partial^2 m_i}{\partial s^2} ds < 0$$

Therefore $\dot{V}(t) \leq 0$ if the conditions (1),(2),(3) holds true. Hence the theorem. ∎

Example: Let us consider an example by choosing the following function in our model (6.1) and (6.2),

$$\mathrm{g}_i(x_i) = r_{1i}\left(1 - \frac{x_i}{x_i}\right), \quad \mathrm{f}_i(y_i) = r_{2i}\left(1 - \frac{y_i}{M_i}\right), \quad \mathrm{p}_i(x_i) = c_{1i}x_i, \; \mathrm{q}_i(y_i) = c_{2i}y_i.$$

$$0 \leq c_{1i}, \; c_{2i} < 1, \; i = 1, 2$$

Then

$$K_i^* = \frac{r_{2i}K_i[r_{1i} - c_{1i}M_i]}{r_{1i}r_{2i} - c_{1i}c_{2i}K_iM_i}, \text{ and } M_i^* = \frac{r_{1i}M_i[r_{2i} - c_{2i}K_i]}{r_{1i}r_{2i} - c_{1i}c_{2i}K_iM_i}$$

From the above it is clear that $K_i^* \leq K_i$ and $M_i^* \leq M_i$.

Here the conditions (1) and (2) of non-linear stability becomes,

$$r_{1i}\left(1 - \frac{x_i + u_i}{K_i}\right) \leq 0, \quad r_{2i}\left(1 - \frac{y_i + v_i}{M_i}\right) \leq 0$$

Now the function $G_i(x_i) = x_i\mathrm{g}_i(x_i)$ is decreasing from the point $x_{0i} = K_i/2$. Similarly the function $F_i(y_i) = y_i\mathrm{f}_i(y_i)$ is starts decreasing from $y_{0i} = M_i/2$.

Now if we choose r_{1i}, r_{2i}, c_{1i}, c_{2i} are such that $x_i^* \geq K_i/2$ and $y_i^* \geq M_i/2$. Then (1) and (2) are satisfied in the following region:

$$\{x_1^* \leq x_i, \; u_i \leq x_2^*, \; y_1^* \leq y_i, \; v_i \leq y_2^*, \text{ for } i = 1, 2\}$$

It is pointed out here that the condition (3) of non linear stability can also satisfied in above region for a suitable choice of $\mathbf{g}_i$, $\mathbf{f}_i$ and $\mathbf{p}_i$ satisfying $\mathbf{H}_1 \to \mathbf{H}_3$. In this particular case the condition (3), becomes

$$x_iy_i\left[c_{1i}u_i - c_{2i}v_i\right]^2 \leq 4r_{1i}r_{2i}u_iv_i\left[1 - \frac{x_i + u_i}{K_i}\right]\left[1 - \frac{y_i + v_i}{M_i}\right] \tag{6.59}$$

This condition is automatically satisfied if for a particular choice of r_{1i}, r_{2i}, c_{1i} and c_{2i}, the maximum of the left hand side is $\leq$ minimum of right hand side. i.e.

$$xx_2^*y_2^*\left[c_{1i}x_2^* - c_{2i}y_1^*\right]^2 \leq 4x_1^*y_1^*r_{1i}r_{2i}\left(\frac{2x_1^*}{K_i} - 1\right)\left(\frac{2y_1^*}{M_i} - 1\right) \tag{6.60}$$

It is clear from (6.60) that for suitable choice of r_{1i} and r_{2i} the above condition can be satisfied. In particular if we take

$$\begin{array}{llll} r_{11} = 0.34, & r_{12} = 0.35, & r_{21} = 0.574, & r_{22} = 0.49, \\ K_1 = 340, & K_2 = 175, & M_1 = 287, & M_2 = 490, \\ c_{11} = 0.0003, & c_{12} = 0.0003, & c_{21} = 0.0001 & c_{22} = 0.0001, \end{array}$$

we get $x_1^* = 250.15, \quad x_2^* = 100, \quad y_1^* = 299.5, \quad y_2^* = 500.$

In this numerical example (6.60) is automatically satisfied.

6.4.4 The Model under Reservoir Boundary Conditions: When $x_2^* > x_1^*$ and $y_1^* > y_2^*$

For $x_2^* > x_1^*$ the monotonicity of steady state solution is similar as in the above case and for $M_1 > M_2$, the monotonicity just reverse of the above case. Hence the steady state solution is monotonic under both set of boundary conditions.

In this case the linear asymptotic stability conditions for the steady state system under reservoir boundary conditions are similar as the above case.

6.4.5 The Model under No-Flux Boundary Conditions: When $x_2^* > x_1^*$ and $y_2^* > y_1^*$

In this section, we study the steady state model with no-flux boundary conditions, i.e.,

$$\frac{du_1(0)}{ds} = 0 = \frac{du_2(L_2)}{ds}; \ \frac{dv_1(0)}{ds} = 0 = \frac{dv_2(L_2)}{ds} \tag{6.61}$$

As before, we assume $x_2^* > x_1^*$ and $y_2^* > y_1^*$.

Let $p_1(s, \alpha_1)$ and $q_1(s, \beta_1)$, $0 \leq s \leq L_1$ be the unique solutions of (6.35) and (6.36) respec-

tively, for i = 1, such that

$$\frac{\partial p_1(0,\alpha_1)}{\partial s} = 0 \ , \ p_1(0,\alpha_1) = \alpha_1 \tag{6.62}$$

$$\frac{\partial q_1(0,\beta_1)}{\partial s} = 0 \ , \ q_1(0,\beta_1) = \beta_1 \tag{6.63}$$

Let $p_2(s,\alpha_2)$ and $q_2(s,\beta)$, $L_1 \leq s \leq L_2$ be the unique solutions of (6.35) and (6.36) respectively, for i = 2, such that

$$\frac{\partial p_2(L_2,\alpha_2)}{\partial s} = 0 \ , \ p_2(L_2,\alpha_2) = \alpha_2 \tag{6.64}$$

$$\frac{\partial q_2(L_2,\beta_2)}{\partial s} = 0 \ , \ q_1(L_2,\beta_2) = \beta_2 \tag{6.65}$$

The existence of the monotonic solutions follows, if we can show that there exists α_1, α_2, β_1 and β_2 such that

$$p_1(L_1,\alpha_1) = p_2(L_1,\alpha_2) \ , \ q_1(L_1,\beta_1) = q_2(L_1,\beta_2) \tag{6.66}$$

$$D_{11}\frac{\partial p_1(L_1,\alpha_1)}{\partial s} = D_{12}\frac{\partial p_2(L_1,\alpha_2)}{\partial s} \tag{6.67}$$

$$D_{21}\frac{\partial q_1(L_1,\beta_1)}{\partial s} = D_{12}\frac{\partial q_2(L_1,\beta_2)}{\partial s} \tag{6.68}$$

From (6.35), multiplying both side by $2du_i/ds$ and integrating w.r.to s from 0 if i=1 and from L_2 if i=2 , we get

$$\left[\frac{du_i}{ds}\right]^2 = -\frac{2}{D_{1i}}\int_{\alpha_i}^{u_i(s)} [u_i \mathrm{g}_i(u_i) - v_i \mathbf{p}_i(u_i)] du_i(s). \tag{6.69}$$

Similarly from (6.36), we have

$$\left[\frac{dv_i}{ds}\right]^2 = -\frac{2}{D_{2i}}\int_{\beta_i}^{u_i(s)} [v_i \mathrm{f}_i(v_i) - u_i \mathbf{q}_i(v_i)] du_i(s). \tag{6.70}$$

As in the case of reservoir boundary conditions, here also similar type of lemmas hold, as stated below :

Lemma 6.4.7 *If* $\alpha_1 > x_1^*$, *then*

$$\frac{\partial p_1(s,\alpha_1)}{\partial s} > 0\ ,\ 0 < s \leq L_1$$

Proof: From (6.69), we get,

$$\left[\frac{\partial p_1(s,\alpha_1)}{\partial s}\right]^2 = -\frac{2}{D_{11}}\int_{\alpha_1}^{p_1(s,\alpha_1)} [p_1 \mathbf{g}_1(p_1) - q_1 \mathbf{p}_1(p_1)]\, dp_1. \tag{6.71}$$

Since $\partial p_1(0,\alpha_1)/\partial s = 0$, $p_1(0,\alpha_1) = \alpha_1$ there exists $s_1 > 0$ such that $p_1(s,\alpha_1) > \alpha_1$ on $0 < s < s_1$. If not, let s_0, $0 < s_0 \leq L_1$, be the first positive value , if it exists, such that $p_1(s_0,\alpha_1) = \alpha_1$. Then by the mean value theorem there exists $\bar{s}$ such that $0 < \bar{s} < s_0$ and $\partial p_1(\bar{s},\alpha_1)/\partial s = 0$; that is,

$$0 = -\frac{2}{D_{11}}\int_{\alpha_1}^{p_1(\bar{s},\alpha_1)} [p_1 \mathbf{g}_1(p_1) - q_1 \mathbf{p}_1(p_1)]\, dp_1 \tag{6.72}$$

But the right-hand side of (6.72) is non-zero,since $p_1 > \alpha_1$ on $0 < s \leq \bar{s}$. Also $\alpha_1 > x_1^*$, therefore, $p_1 > x_1^*$. This implies that, $p_1 \mathbf{g}_1(p_1) - q_1 \mathbf{p}_1(p_1) < 0$, giving a contradiction. Hence $p_1(s,\alpha_1) > \alpha_1$, for all value $0 < s \leq L_1$. This implies, $p(s,\alpha_1) > x_1^*$, on $0 < s \leq L_1$. Hence by (6.33) and (6.71),the result follows. ∎

Similarly by using (6.70) and (6.34) the following lemma follows:

Lemma 6.4.8 *If* $\beta_1 > y_1^*$, *then*

$$\frac{\partial q_1(s,\beta_1)}{\partial s} > 0\ ,\ 0 < s \leq L_1$$

Lemma 6.4.9 *If* $0 < p_2(s,\alpha_2) \leq x_2^*$, *then* $\alpha_2 < x_2^*$ *implies* $p_2(s,\alpha_2) < \alpha_2$, *for* $L_1 \leq s < L_2$.

Proof: Since $0 < p_2(s, \alpha_2) \leq x_2^*$, then from (6.33), we get, $p_2 g_2(p_2) - q_2 P_2(p_2) > 0$. Now, since $\alpha_2 < x_2^*$, then $p_2 g_2(p_2) - q_2 P_2(p_2) > 0$, for all α_2, p_2. Hence, from (6.69), $p_2 < \alpha_2$. ∎

Again by using (6.70) and (6.34) the following lemma follows:

Lemma 6.4.10 *If $0 < q_2(s, \beta_2) \leq y_2^*$, then $\beta_2 < y_2^*$ implies $q_2(s, \beta_2) < \beta_2$, for $L_1 \leq s < L_2$.*

Lemma 6.4.11 *Define $G_{1i}(\alpha_i)$ by $G_{1i}(\alpha_i) = p_i(L_1, \alpha_i)$. Then there exists $\hat{\alpha}_i > 0$, such that*

$$\begin{aligned} \mathrm{G}_{11} &: [x_1^*, \hat{\alpha}_1] \rightarrow [x_1^*, x_2^*], \\ \mathrm{G}_{12} &: [\hat{\alpha}_2, x_2^*] \rightarrow [x_1^*, x_2^*]. \end{aligned}$$

Lemma 6.4.12 *Define $G_{2i}(\beta_i)$ by $G_{2i}(\beta_i) = q_i(L_1, \beta_i)$. Then there exists $\hat{\beta}_i > 0$, such that*

$$\begin{aligned} \mathrm{G}_{21} &: \left[y_1^*, \hat{\beta}_1\right] \rightarrow [y_1^*, y_2^*], \\ \mathrm{G}_{22} &: \left[\hat{\beta}_2, y_2^*\right] \rightarrow [y_1^*, y_2^*]. \end{aligned}$$

Proof: Same as Lemma 2.3.6 in chapter 2. ∎

Theorem 6.4.8 *(i) There exists a continuous, monotonic solution of system (6.35) with continuous flux at L_1.*

(ii) There exists a continuous, monotonic solution of system (6.36) with continuous flux at L_1.

Proof: Analogous to theorem 2.3.5 in chapter 2 ∎

Finally, in a similar manner as in the case of the reservoir boundary conditions, the following linear and nonlinear stability theorems can be proved.

Theorem 6.4.9 *The steady-state, continuous, monotonic solutions of system (6.35) and (6.36) with continuous flux at the interface $s = L_1$ is asymptotically stable provided the following conditions are satisfied:*

$$(i) \quad \frac{d}{du_i}\left[u_i \mathrm{g}_i(u_i)\right] \leq 0 \ ,$$

$$(ii) \quad \frac{d}{dv_i}\left[v_i \mathrm{f}_i(v_i)\right] \leq 0 \ , \text{ and}$$

$$(iii) \quad \left[\mathrm{p}_i(u_i) + \mathrm{q}_i(v_i)\right]^2 < 4\left[\frac{d}{du_i}\left[u_i \mathrm{g}_i(u_i)\right]\right]\left[\frac{d}{dv_i}\left[v_i \mathrm{f}_i(v_i)\right]\right]$$

for $x_1^* \leq u_i \leq x_2^*, \quad y_1^* \leq v_i \leq y_2^*$ *and* $i = 1, 2$.

Theorem 6.4.10 *The steady-state ,continuous ,monotonic solutions of non-linear system (6.35), (6.36), (6.51) and (6.61), with continuous flux at the interface $s = L_1$ is asymptotically stable in the subregion of* **R***:*

$$\{x_1^* \leq x_i, \ u_i \leq x_2^*, \ y_1^* \leq y_i \ v_i \leq y_2^*, \ \text{for } i = 1, 2\}$$

provided the following conditions are satisfied:

$$(1) \quad \frac{x_i \mathrm{g}_i(x_i) - u_i \mathrm{g}_i(u_i)}{x_i - u_i} \leq 0 \ ,$$

(2) $\dfrac{y_i f_i(y_i) - v_i f_i(v_i)}{y_i - v_i} \leq 0$,

(3) $x_i y_i \left[\dfrac{u_i p_i(x_i)}{x_i} + \dfrac{v_i q_i(y_i)}{y_i}\right]^2 < 4u_i v_i \left[\dfrac{x_i g_i(x_i) - u_i g_i(u_i)}{x_i - u_i}\right]\left[\dfrac{y_i f_i(y_i) - v_i f_i(v_i)}{y_i - v_i}\right]$

Remark: The above theorems imply that the system will settle down to a steady state distribution for each species, in the two patches under certain conditions, the magnitude of the steady state distributions of both the species being lower than it's initial density. The above analysis also suggest that patchiness destabilizes the system which we can note by comparing the results with the uniform steady state case, [see section 6.4.1].

6.4.6 Both The Species have Uniform Steady State In The Second Patch:

In this case, the steady-state solutions of both the species are non-uniform in the first patch and constant in second patch, i.e. $u_2 = x_2^*$ and $v_2 = M_2$, $L_1 \leq s \leq L_2$, $t \geq 0$. As shown in the general case we note that here also the steady state solution is positive, continuous and monotonic in the first patch. For stability analysis we use the positive definite function,

$$\begin{aligned} V(t) &= \int_0^{L_1} (x_1 - u_1)^2\, ds + \int_{L_1}^{L_2} (x_2 - u_2)^2\, ds \\ &+ \int_0^{L_1} (y_1 - v_1)^2\, ds + \int_{L_1}^{L_2} (y_2 - v_2)^2\, ds \end{aligned} \tag{6.73}$$

and analyze in the similar manner as in Theorem 6.4.3 and Theorem 6.4.7, and can prove the following theorem,

Theorem 6.4.11 *Let $u_2 = x_2^*$ and $v_2 = y_2^*$. Then the steady-state, continuous, monotonic solutions of non-linear system (6.1) to (6.7) and with either (6.8) or (6.9)and with continuous flux at the interface $s = L_1$ is asymptotically stable in a subregion of $\mathcal{R}$: $\{K_1 \leq x_1 \leq K_2$,*

$x_1^* \leq u_1 \leq x_2^*,\ M_1 \leq y_1, v_1 \leq M_2$ }, *provided the following conditions are satisfied:*

(1) $$\frac{x_1 g_1(x_1) - u_1 g_1(u_1)}{x_1 - u_1} \leq 0\,,$$

(2) $$\frac{y_1 f_1(y_1) - v_1 f_1(v_1)}{y_1 - v_1} \leq 0\,,$$

(3) $$\frac{u_1 [p_1(x_1)]^2}{x_1} \leq 4\frac{v_1}{y_1}\left[\frac{x_1 g_1(x_1) - u_1 g_1(u_1)}{x_1 - u_1}\right]\left[\frac{y_1 f_1(y_1) - v_1 f_1(v_1)}{y_1 - v_1}\right]$$

Similar as the prey-predator system, the conditions of the above theorem 6.4.11 are less in number then the conditions of non-linear stability in the general nonuniform case in two-patch habitat and more in number then the uniform case.

6.5 Numerical Examples

Now we show the existence of positive, monotonic, continuous steady state solutions of the system with reservoir boundary condition and flux matching condition at the interface by considering the following example corresponding to systems (6.35) and (6.36), .

$$D_{1i}\frac{d^2 u_{1i}}{dx^2} = (a_{1i} - b_{1i}u_{1i} - c_{1i}u_{2i})\, u_{1i} \tag{6.74}$$

$$D_{1i}\frac{d^2 u_{2i}}{dx^2} = (a_{2i} - b_{2i}u_{2i} - c_{2i}u_{1i})\, u_{2i} \tag{6.75}$$

The reservoir boundary conditions are:

$$u_{11}(0) = x_1^*, \quad u_{12}(L_2) = x_2^*, \tag{6.76}$$

$$u_{21}(0) = y_1^*, \quad u_{22}(L_2) = y_2^* \tag{6.77}$$

The continuous flux matching conditions at the interface are

$$D_{11}\frac{du_{11}(L_1)}{dx} = D_{12}\frac{du_{12}(L_1)}{dx}, \tag{6.78}$$

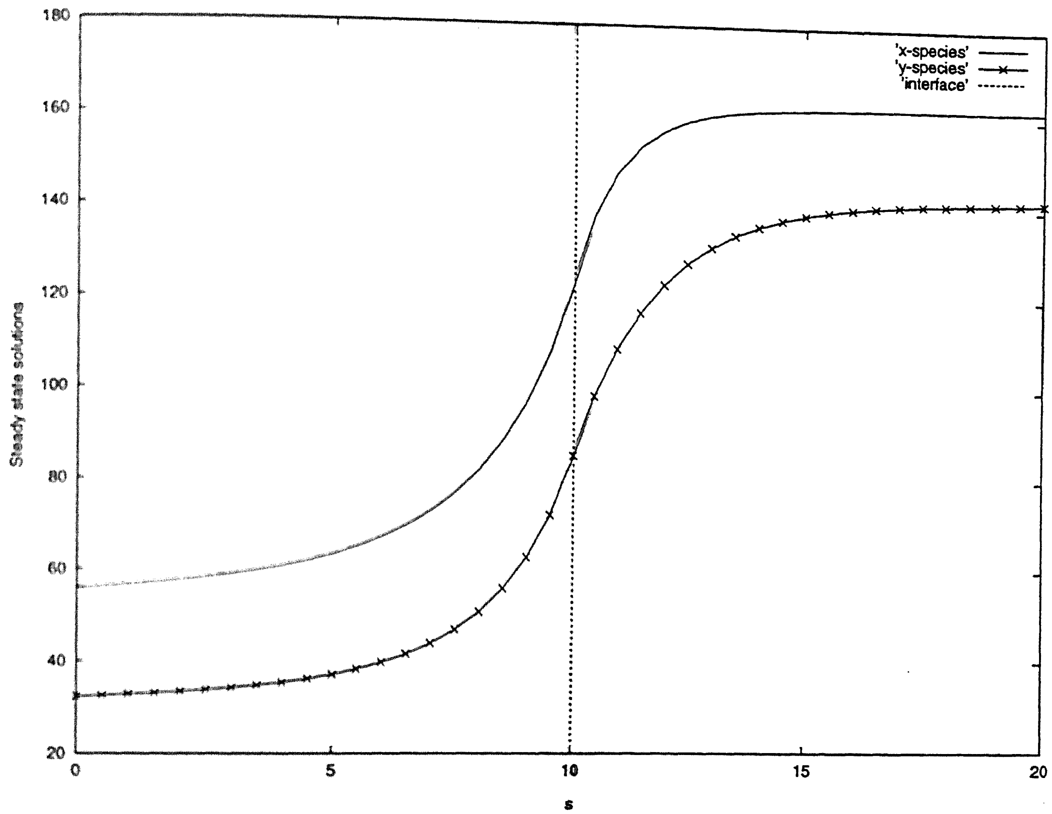


Figure 6.3: The steady state solutions, when $x_2^* = 162.162 > x_1^* = 55.882$, $y_2^* = 141.892 > y_1^* = 32.353$

$a_{11} = 0.115$	$a_{12} = 0.825$	$a_{21} = 0.135$	$a_{22} = 0.3$
$b_{11} = 0.002$	$b_{12} = 0.005$	$b_{21} = 0.004$	$b_{22} = 0.002$
$c_{11} = 0.0001$	$c_{12} = 0.0001$	$c_{21} = 0.0001$	$c_{22} = 0.0001$
$D_{11} = 0.75$	$D_{12} = 0.8$	$D_{21} = 0.75$	$D_{22} = 0.8$

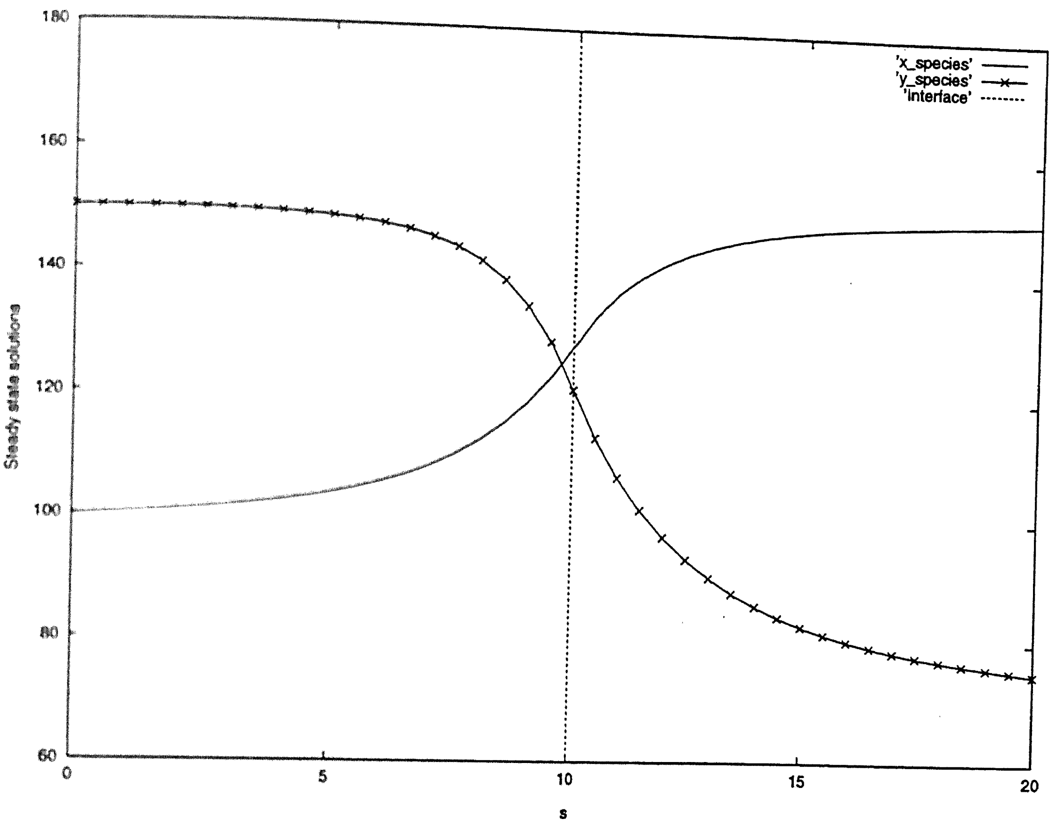


Figure 6.4: The steady state solutions, when $x_1^* = 100.0 < x_2^* = 149.99$, $y_2^* = 74.999 < y_1^* = 149.99$

$a_{11} = 0.275$	$a_{12} = 0.825$	$a_{21} = 0.63$	$a_{22} = 0.3$
$b_{11} = 0.002$	$b_{12} = 0.005$	$b_{21} = 0.004$	$b_{22} = 0.002$
$c_{11} = 0.0005$	$c_{12} = 0.001$	$c_{21} = 0.0003$	$c_{22} = 0.001$
$D_{11} = 1.2$	$D_{12} = 1.2$	$D_{21} = 1.2$	$D_{22} = 1.2$

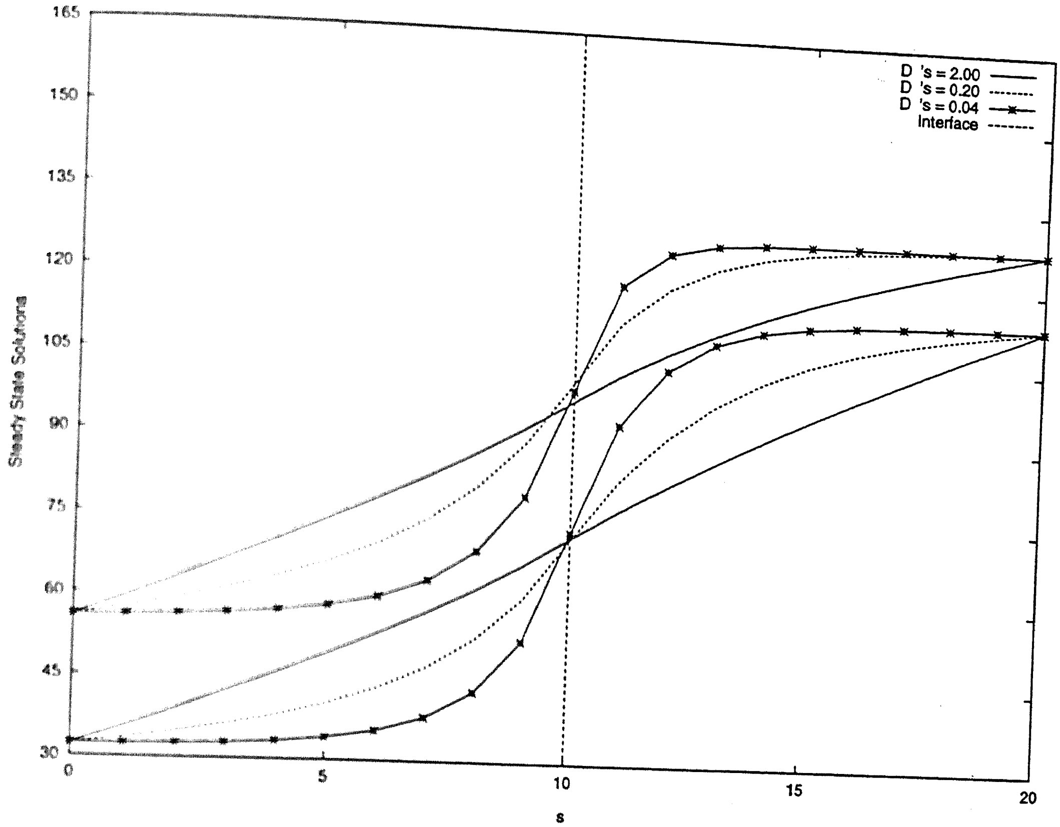


Figure 6.5: Effects of diffusion coefficients in steady state solutions, when $x_1^* = 55.882 < x_2^* = 127.728$, $y_1^* = 32.353 < y_2^* = 113.614$

$a_{11} = 0.0115$	$a_{12} = 0.0625$	$a_{21} = 0.0135$	$a_{22} = 0.024$
$b_{11} = 0.0002$	$b_{12} = 0.0005$	$b_{21} = 0.0004$	$b_{22} = 0.0002$
$c_{11} = 1.00E-05$	$c_{12} = 1.00E-05$	$c_{21} = 1.00E-05$	$c_{22} = 1.00E-05$

$$D_{21}\frac{du_{21}(L_1)}{dx} = D_{22}\frac{du_{22}(L_1)}{dx}, \tag{6.79}$$

$$u_{11}(L_1) = u_{12}(L_1), \quad u_{21}(L_1) = u_{22}(L_1). \tag{6.80}$$

We have solved system of equations (6.74) to (6.80) numerically using finite difference method in various cases for different set of parameters statisfing the stability conditions and the corresponding graphs are shown in Fig.6.3, Fig.6.4 and Fig.6.5.

From the above graphs it can be noted that in all the cases the steady state solution is positive, continuous and monotonic. In particular from Fig.6.3 and 6.4, we see that for all possible combination of x_i^*'s and y_i^*'s, the steady state solutions are monotonic. In Fig.6.5, the effects of diffusion coefficients on the non-uniform steady state distributions are shown and it is noted that as diffusion coefficients becomes vary large in both the patches, the steady state solutions tends towards linear distributions.

6.6 Summary

In this chapter, we have considered a general competition model of two species with diffusion in a two patch environment. The model has been given by a system of two autonomous partial differential equations. We have obtained the existence of the positive, monotonic, continuous steady-state solution for each species, with continuous flux at the interface. The conditions for asymptotic stability both linear and non-linear model cases under both reservoir or no-flux boundary conditions have been derived. It has been shown that in both cases the non-uniform steady-state is asymptotically stable under appropriate conditions. It is also shown that the uniform steady-state of the system is globally asymptotically stable under less stringent conditions. It is further noted that the patchiness destabilizes the non-uniform steady state which can be seen by comparing the results (stability conditions) with corresponding to uniform steady state, as in the case of prey-predator system in chapter-4.

Bibliography

1. **Allen, L.J.S.**, *Persistence and extinction in single-species reaction-diffusion models*, Bul. Math. Biol., **45**, 209-227 (1983).

2. **Allen, L.J.S.**, *Persistence and extinction in Lotka-Volterra reaction-diffusion equations*, Math. Biosci., **65**, 1-12 (1983).

3. **Freedman, H.I.** and **Krisztin** , *Global stability in model of population dynamics with diffusion. I. Patchy Environment*, Proc. Royal Soci. of Edinburgh, **122A**, 69-84 (1992).

4. **Freedman, H.I.**, **Shukla, J.B.** and **Takeuchi, Y.**, *Population diffusion in a two-patch environment*, Mathl. Biosci., **95**, 111-123 (1989).

5. **Freedman, H.I.** and **Shukla, J.B.**: *The effect of a predator resource on a diffusive predator-prey system*, Natural Resou. Modelling, **3**(3), (1989).

6. **Freedman, H.I.** and **Rai, B.**, *Uniform persistence and global stability in models involving mutualism 1. Predator-prey-mutualistic systems*, Mathematical Modelling of Environmental and Ecological Systems,(Shukla, J.B., Hallam, T.G. and Capasso,V., eds.), Elsevier Sci.Publ., Amsterdam, 193-202 (1987).

7. **Freedman, H.I.** and **So, J.W.H.**, *Global stability and persistence of simple food chains*, Mathl. Biosci., **76**, 69-86 (1985).

8. **Freedman, H.I.** and **Wu, J.**, *Steady state analysis in a model for population diffusion in a multi-patch environment*, Nonl. Analy., Theor., Meths. & Appl., **18**(6), 517-542 (1992).

9. **Gopalsamy, K.**, *Competition,dispersion and co-existence*, Math. Bio. Sci., **33**, 25-33 (1977).

10. **Hadeler, K.P.**, **Heiden, V.** and **Rothe, F.**, *Nonhomogeneous spatial distributions of populations*, J. Math. Biol., **1**, 165-176 (1974).

11. **Hastings, A.**, *Global stability in Lotka-Volterra systems with diffusion*, J. Math. Biol., **6**, 163-168 (1978).

12. **Hallam, T.G.**, *A temporal study of diffusion effects on a population modelled by quadratic growth*, Nonl. Anal. Theor. Meths. Appl., **3**, 123-133 (1979).

13. **Kapur, J.N.**, *Diffusive instability for diffusion reaction systems in finite domains*, J. Math. Phy. Sci., **17**, 483-495 (1984).

14. **Levin, S.A.**, *Population model and community structure in hetrogeneous environments*, in *Mathematical Ecology*, Hallam, T.G. and Levin, S.A., eds., Springer, New York, 295-321 (1986).

15. **McMurtrie, R.**, *Persistence and stability of single species and prey-predator system in spatially hetrogeneous environments*, Mathl. Biosci., **39**, 11-51 (1978).

16. **Okubo, A.**, *Diffusion and Ecological Problem: Mathematical models*, Lecture Notes, Springer-Verlag (1980).

and

17. **Pao, C.V.**, *Coexistence and stability of a competition diffusion system in population dynamics*, J. Math. Anal. Appl., **83**, 54-76 (1981).

18. **Rothe, F.**, *Global Solution of Reaction-Diffusion Systems*, Lecture Notes in Mathematics, 1072, Springer-Verlag (1984).

19. **Shukla, J.B.** and **Verma, S.**, *Effects of convective and dispersive interactions on the stability of two species*, Bul. Math. Biol., **43**, 593-610 (1981).

20. **Shukla, V.P.**, **Shukla, J.B.** and **Das, P.C.**, *Environmental effects on the linear stability of a three species food chain model*, Mathl. Biosci., **57**, 35-58 (1981).

21. **Skellam, J.G.**, *Random dispersal in theoretical populations*, Biometrika, **36**, pp.199-218 (1951).

Chapter 7

A Competing Species Model with Diffusion and a Common Supplementary Resource for Both the Species in a Two-Patch Habitat

7.1 Introduction

As discussed in chapters 3 and 5, the study of resource-based competition model is an important area of research in population biology. Some experimental investigations on micro-organisms using the chemostat [9, 17] have been conducted in fifties and perhaps the best laboratory idealization of nature for population studies has been described in [22]. Several mathematical models of such systems, involving competition and other types of non-interacting populations which depend upon growth limiting nutrient in a chemostat with constant input and variable washout rates have been studied [1, 11, 13]. Also a few other mathematical investigations related to two competing populations which are wholly dependent on a self-renewable resource in a habitat without diffusion have been conducted [7, 10, 16].

It may be noted here, that though the effect of diffusion on the growth and co-existence of interacting species have been discussed by several investigators [4, 15, 18, 19, 20, 21], very little attention has been paid to study such problems with alternative or supplementary resource and diffusion. Recently Freedman and Shukla [4] have studied the effect of an alternative resource for predator on a prey-predator system with diffusion in a homogeneous habitat.

It may be noted that in the above studies, the effect of patchiness on population coexistence with diffusion in each patch has not been considered. Though, Freedman et al., [2, 3, 6] studied a single species diffusion model by assuming that the habitat consists of two patches and shown that the steady-state solutions are monotonic and the asymptotic stability conditions under both reservoir and no-flux boundary conditions but they did study the resource-based population model. They have neither considered the effect of patchiness on two interacting populations, nor the role of supplementary resource in patchy habitat.

Keeping in view the above and noting the discussion in chapter-6, in this chapter, we study the effect of a common supplementary resource on the coexistence of two competing species with diffusion, in a two patch habitat. This chapter is organized as follows, first we write the complete model of two competing species with a common supplementary resource in a two-patch habitat in section 7.2. In the next section, we study our main model in a two-patch habitat for both non-uniform and uniform steady state cases under both reservoir and no-flux boundary conditions.

7.2 Mathematical Model

We consider a general model of two competing species diffusing between two homogeneous patches in a given habitat as discussed in the chapter-6. We consider further that there is a common non-diffusing self-renewable resource for both the species in the two patches.

Let $R_i(s,t)$, $x_i(s,t)$ and $y_i(s,t)$ $(i = 1, 2)$, be the resource biomass density and populations densities of two species competing for this resource, such that each species logistically grows in the absence of the other species, and the rate of growth of each species decreases due to the presence of the other species in the i-th patch. We assume that the density of each of the competing populations increases with the increase in the density of the supplementary resource biomass and corresponding resource biomass density decreases. The system, is then, governed by the following autonomous partial differential equations:

$$\frac{\partial R_i}{\partial t} = a_i R_i \left(1 - \frac{R_i}{C_i}\right) - \alpha_i R_i x_i - \beta_i R_i y_i \tag{7.1}$$

$$\frac{\partial x_i}{\partial t} = x_i \mathrm{g}_i(x_i) - y_i \mathrm{p}_i(x_i) + \theta \alpha_i R_i x_i + D_{1i} \frac{\partial^2 x_i}{\partial s^2} \tag{7.2}$$

$$\frac{\partial y_i}{\partial t} = y_i \mathrm{f}_i(y_i) - x_i \mathrm{q}_i(y_i) + \phi \beta_i R_i y_i + D_{2i} \frac{\partial^2 y_i}{\partial s^2} \tag{7.3}$$

$$0 \leq s \leq L_2, \quad \text{and } i = 1, 2.$$

where the i-th patch is assumed to lie along the spatial length $L_{i-1} \leq s \leq L_i$ $(L_0 = 0)$, C_i, $i = 1, 2$ is the carrying capacity of the supplementary resource in the i-th patch and the constants α_i and β_i, $i = 1, 2$, are positive interaction rate coefficients of the alternative resource with the first (x_i) and second (y_i) species respectively in the i-th patch. The functions $\mathrm{g}_i(x_i)$ and $\mathrm{f}_i(y_i)$ are the respective specific growth rates, $\mathrm{p}_i(x_i)$, $\mathrm{q}_i(y_i)$ are interaction rates of $x_i(s,t)$ and $y_i(s,t)$, and D_{1i}, D_{2i} are the diffusion coefficients of x_i and y_i in the i-th patch respectively. The constants θ and ϕ are the conversion rate coefficients for the first (x_i) and second (y_i) species respectively.

We assume the following assumption for $\mathrm{g}_i(x_i)$, $\mathrm{f}_i(y_i)$, $\mathrm{p}_i(x_i)$ and $\mathrm{q}_i(y_i)$

When the first (x_i) and second (y_i) species have carrying capacity K_i, M_i respectively in the i-th patch, then $g_i(K_i) = 0$, $f_i(M_i) = 0$, $i = 1, 2$. Further we assume that,

AH_2: $\exists\ R_i^*, x_i^{**}, y_i^{**} > 0$, such that

$$R_i^* = C_i[a_i - \alpha_i x_i^{**} - \beta_i y_i^{**}]/a_i$$

$$x_i^{**} g_i(x_i^{**}) - y_i^{**} p_i(x_i^{**}) + \theta \alpha_i R_i^* x_i^{**} = 0$$

$$y_i^{**} f_i(y_i^{**}) - x_i^{**} q_i(y_i^{**}) + \phi \beta_i R_i^* y_i^{**} = 0$$

The model is studied under two set of boundary conditions i.e. reservoir and no-flux. In the case of reservoir boundary conditions, we take

$$x_1(0,t) = x_1^{**}\ ,\ x_2(L_2,t) = x_2^{**} \tag{7.4}$$

$$y_1(0,t) = y_1^{**}\ ,\ y_2(L_2,t) = y_2^{**} \tag{7.5}$$

and in the case of no-flux boundary conditions, we have

$$\frac{\partial x_1(0,t)}{\partial s} = 0 = \frac{\partial x_2(L_2,t)}{\partial s}, \tag{7.6}$$

$$\frac{\partial y_1(0,t)}{\partial s} = 0 = \frac{\partial y_2(L_2,t)}{\partial s}. \tag{7.7}$$

We also assume the continuity and flux matching conditions at the interface $s = L_1$. The continuity conditions at the interface $s = L_1$ for this system are,

$$x_1(L_1,t) = x_2(L_1,t),\ \ y_1(L_1,t) = y_2(L_1,t) \ \text{ and } \ R_1(L_1,t) = R_2(L_1,t) \tag{7.8}$$

The continuous flux matching conditions at the interface $s = L_1$ for $x_i(s,t)$ and $y_i(s,t)$ are written as,

$$D_{11}\frac{\partial x_1(L_1,t)}{\partial s} = D_{12}\frac{\partial x_2(L_1,t)}{\partial s} \tag{7.9}$$

$$D_{21}\frac{\partial v_1(L_1,t)}{\partial s} = D_{22}\frac{\partial v_2(L_1,t)}{\partial s} \tag{7.10}$$

Finally, the model is completed by assuming some positive initial distribution of each species, for $i = 1, 2$, that is,

$$x_i(s,0) = \chi_i(s) > 0, \;\; L_{i-1} < s < L_i \tag{7.11}$$

$$y_i(s,0) = \delta_i(s) > 0, \;\; L_{i-1} < s < L_i \tag{7.12}$$

$$R_i(s,0) = R_{0i}(s) > 0, \;\; L_{i-1} < s < L_i. \tag{7.13}$$

Our main aim is to study the long time behavior of the uniform and nonuniform steady state solution of the above model under both type of boundary conditions (namely, reservoir and no flux) and the continuous flux matching conditions at the interface of the two patches.

7.3 Analysis of the Model in a Two Patch Habitat

7.3.1 The Non-uniform Steady State: Under Both Sets of Boundary Conditions

Let $w_i(s)$, $u_i(s)$ and $v_i(s)$ be the steady state solutions of the supplementary resource (R_i), first species (x_i) and second species (y_i). Then the steady state system of the above proposed model becomes,

$$w_i = \frac{C_i}{a_i}\left[a_i - \alpha_i u_i - \beta_i v_i\right] \tag{7.14}$$

$$D_{1i}\frac{d^2u_i}{ds^2} + u_i\mathrm{g}_i(u_i) - v_i\mathrm{p}_i(u_i) + \theta\alpha_i w_i u_i = 0 \tag{7.15}$$

$$D_{2i}\frac{d^2v_i}{ds^2} + v_i\mathrm{f}_i(v_i) - u_i\mathrm{q}_i(v_i) + \phi\beta_i w_i v_i = 0 \tag{7.16}$$

Now substituting the value of w_i from (7.14) into (7.15) and (7.16), we get,

$$D_{1i}\frac{d^2u_i}{ds^2} + u_i\mathcal{G}_i(u_i) - v_i\mathcal{P}_i(u_i) = 0 \tag{7.17}$$

$$D_{2i}\frac{d^2v_i}{ds^2} + v_i\mathcal{F}_i(v_i) - u_i\mathcal{Q}_i(v_i) = 0 \tag{7.18}$$

where,

$$\begin{aligned}
\mathcal{G}_i(u_i) &= \mathrm{g}_i(u_i) + \theta\alpha_i\frac{C_i}{a_i}(a_i - \alpha_i u_i),\\
\mathcal{P}_i(u_i) &= \mathrm{p}_i(u_i) + \theta\alpha_i\beta_i\frac{C_i}{a_i}u_i,\\
\mathcal{F}_i(v_i) &= \mathrm{f}_i(v_i) + \phi\beta_i\frac{C_i}{a_i}(a_i - \beta_i v_i),\\
\mathcal{Q}_i(v_i) &= \mathrm{q}_i(v_i) + \phi\alpha_i\beta_i\frac{C_i}{a_i}v_i.
\end{aligned}$$

Again the functions $\mathcal{G}_i(u_i)$ and $\mathcal{F}_i(v_i)$ are logistic type, since
$\mathcal{G}_i(0) = \mathrm{g}_i(0) + \theta\alpha_i C_i > 0,\quad \mathcal{G}_i'(u_i) = \mathrm{g}_i'(u_i) - \theta\alpha_i^2 C_i/a_i \le 0,\ \forall u_i \neq 0$
$\mathcal{F}_i(0) = \mathrm{f}_i(0) + \phi\beta_i C_i > 0,\quad \mathcal{F}_i'(v_i) = \mathrm{f}_i'(v_i) - \phi\beta_i^2 C_i/a_i \le 0,\ \forall v_i \neq 0.$
Also, since
$\mathcal{P}_i(0) = 0,\ \mathcal{P}_i'(u_i) \le 0\ \forall u_i \neq 0$ and
$\mathcal{Q}_i(0) = 0,\ \mathcal{Q}_i'(v_i) \le 0\ \forall v_i \neq 0,$
therefore the functions $\mathcal{P}_i(u_i)$ and $\mathcal{Q}_i(v_i)$ are interaction type functions as considered in chapter-6. Further, the assumption $\mathbf{H_3}$ of the chapter 6, is now modified as,
$\exists\ x_i^{**}, y_i^{**} > 0$, such that,

$$x_i^{**}\mathcal{G}_i(x_i^{**}) - y_i^{**}\mathcal{P}_i(x_i^{**}) = 0, \tag{7.19}$$

$$y_i^{**}\mathcal{F}_i(y_i^{**}) - x_i^{**}\mathcal{Q}_i(y_i^{**}) = 0, \tag{7.20}$$

We also assume as in chapter-4,5,6, the following conditions,

$$(x_i - x_i^{**})[x_i\mathrm{g}_i(x_i) - y_i\mathrm{p}_i(x_i)] < 0,\ \forall x_i \neq x_i^{**} \text{ and } min\{y_1^{**}, y_2^{**}\} \le y_i \le max\{y_1^{**}, y_2^{**}\} \tag{7.21}$$

$$(y_i - y_i^{**})[y_i\mathrm{f}_i(y_i) - x_i\mathrm{q}_i(y_i)] < 0,\ \forall y_i \neq y_i^{**} \text{ and } min\{x_1^{**}, x_2^{**}\} \le x_i \le max\{x_1^{**}, x_2^{**}\} \tag{7.22}$$

is valid throughout the chapter.

Then the system (7.17) and (7.18) with boundary conditions,

$$u_1(0,t) = x_1^{**},\ u_2(L_2,t) = x_2^{**} \text{ and } v_1(0,t) = y_1^{**},\ v_2(L_2,t) = y_2^{**} \tag{7.23}$$

or

$$\frac{\partial u_1(0,t)}{\partial s} = 0 = \frac{\partial u_2(L_2,t)}{\partial s}, \text{ and } \frac{\partial v_1(0,t)}{\partial s} = 0 = \frac{\partial v_2(L_2,t)}{\partial s}, \tag{7.24}$$

and the continuity and flux matching conditions at the interface $s = L_1$,

$$u_1(L_1,t) = u_2(L_1,t),\ \ v_1(L_1,t) = v_2(L_1,t) \tag{7.25}$$

$$D_{11}\frac{du_1}{ds}(L_1) = D_{12}\frac{du_2}{ds}(L_1), \text{ and } D_{21}\frac{dv_1}{ds}(L_1) = D_{22}\frac{dv_2}{ds}(L_1), \tag{7.26}$$

become exactly of the same type of steady state system, as described in chapter-6.

Remark: Since we are only interested in the positive steady state of the system, therefore, $u_i < a_i/\alpha_i$ and $v_i < a_i/\beta_i$ and hence
$\mathcal{G}_i(u_i) \geq \mathrm{g}_i(u_i),\ \forall\ u_i$ and $\mathcal{P}_i(u_i) \geq \mathrm{p}_i(u_i),\ \forall\ u_i$,
$\mathcal{F}_i(u_i) \geq \mathrm{f}_i(u_i),\ \forall\ u_i$ and $\mathcal{Q}_i(u_i) \geq \mathrm{q}_i(u_i),\ \forall\ u_i$

Thus, in presence of the non-diffusing, self-renewable supplementary resource, the steady state problem becomes the same type of steady state system of two competing species as in chapter-6, with the modified growth rates $\mathcal{G}_i(u_i)$ and $\mathcal{F}_i(v_i)$ and the modified interaction rates $\mathcal{P}_i(u_i)$ and $\mathcal{Q}_i(v_i)$. Therefore, the behavior of the steady state solutions will be same as in chapter-6. Now, exactly in similar manner, we can state and prove the following theorem,

Theorem 7.3.1 *(i) There exists a positive, continuous, monotonic steady state solution u_i for the x_i species with continuous flux at L_1.*

(ii) There exists a positive, continuous, monotonic steady state solution v_i for the y_i species with continuous flux at L_1.

Now we go for the linear and nonlinear stability of the system, which will be different from the case studied in chapter-6.

Theorem 7.3.2 *The steady state, continuous, monotonic solutions of the linearized system (7.1)-(7.2) with reservoir boundary and continuous flux matching conditions at the interface* $s = L_1$ *is asymptotically stable provided the following conditions are satisfied:*

$$(i) \quad \mathcal{X}_i \leq 0,\ \mathcal{Y}_i \leq 0,\ \mathcal{Z}_i \leq 0 \tag{7.27}$$

$$(ii) \quad \mathcal{U}_i^2 \leq 4\mathcal{X}_i\mathcal{Y}_i \tag{7.28}$$

$$(iii) \quad \mathcal{X}_i\mathcal{Y}_i\mathcal{Z}_i + 2\mathcal{U}_i\mathcal{V}_i\mathcal{W}_i \leq \mathcal{X}_i\mathcal{V}_i^2 + \mathcal{Y}_i\mathcal{W}_i^2 + \mathcal{Z}_i\mathcal{U}_i^2. \tag{7.29}$$

where

$$\begin{aligned}
\mathcal{X}_i &= \mathrm{g}_i(u_i) + u_i\mathrm{g}_i'(u_i) - v_i\mathrm{p}_i'(u_i) + \theta\alpha_i w_i, & \mathcal{Y}_i &= \mathrm{f}_i(v_i) + v_i\mathrm{f}_i'(v_i) - u_i\mathrm{q}_i'(v_i) + \phi\beta_i w_i,\\
\mathcal{Z}_i &= a_i\left(1 - \frac{2w_i}{C_i}\right) - \alpha_i u_i - \beta_i v_i, & \mathcal{U}_i &= -\frac{1}{2}[\mathrm{p}_i(u_i) + \mathrm{q}_i(v_i)],\\
\mathcal{V}_i &= \frac{\beta_i}{2}[\phi v_i - w_i], \ \textit{and} & \mathcal{W}_i &= \frac{\alpha_i}{2}[\theta u_i - w_i]
\end{aligned} \tag{7.30}$$

Proof: Linearizing (7.1), (7.2) and (7.3) by using,

$$R_i(s,t) = w_i(s) + r_i(s,t) \tag{7.31}$$

$$x_i(s,t) = u_i(s) + n_i(s,t) \tag{7.32}$$

$$y_i(s,t) = v_i(s) + m_i(s,t) \tag{7.33}$$

we have,

$$\frac{\partial r_i}{\partial t} = r_i\left[a_i\left(1 - \frac{2w_i}{C_i}\right) - \alpha_i u_i - \beta_i v_i\right] - n_i\alpha_i w_i - m_i\beta_i w_i \tag{7.34}$$

$$\frac{\partial n_i}{\partial t} = n_i[\mathrm{g}_i(u_i) + u_i\mathrm{g}_i'(u_i) - v_i\mathrm{p}_i'(u_i) + \theta\alpha_i w_i] - m_i\mathrm{p}_i(u_i) + r_i\theta\alpha_i u_i + D_{1i}\frac{\partial^2 n_i}{\partial s^2} \tag{7.35}$$

$$\frac{\partial m_i}{\partial t} = m_i[\mathrm{f}_i(v_i) + v_i\mathrm{f}_i'(v_i) - u_i\mathrm{q}_i'(v_i) + \phi\beta_i w_i] - n_i\mathrm{q}_i(v_i) + r_i\phi\beta_i v_i + D_{2i}\frac{\partial^2 m_i}{\partial s^2} \tag{7.36}$$

Using (7.31), (7.32) and (7.33), the corresponding boundary and matching conditions can be obtained as follows,

$$\begin{aligned}
n_1(0,t) &= 0 = n_2(L_2,t),\; m_1(0,t) = 0 = m_2(L_2,t) \quad (\text{ Reservoir case }) \\
\frac{\partial n_1}{\partial s}(0,t) &= \frac{\partial n_2}{\partial s}(L_2,t),\; \frac{\partial m_1}{\partial s}(0,t) = \frac{\partial m_2}{\partial s}(L_2,t) \quad (\text{ No-flux case }) \\
n_1(L_1,t) &= 0 = n_2(L_1,t),\; m_1(L_1,t) = 0 = m_2(L_1,t) \\
D_{11}\frac{\partial n_1}{\partial s}(L_1,t) &= D_{12}\frac{\partial n_2}{\partial s}(L_1,t),\; D_{21}\frac{\partial m_1}{\partial s}(L_1,t) = D_{22}\frac{\partial m_2}{\partial s}(L_1,t).
\end{aligned}$$

Now, we consider the following positive definite function,

$$V(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \frac{1}{2}[r_i^2 + n_i^2 + m_i^2]ds \tag{7.37}$$

From which we get,

$$\dot{V}(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \left[r_i\frac{\partial r_i}{\partial t} + n_i\frac{\partial n_i}{\partial t} + m_i\frac{\partial m_i}{\partial t} \right] ds$$

By using (7.35), (7.36) and (7.34), we get,

$$\begin{aligned}
\dot{V}(t) = \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} r_i^2 \left[a_i\left(1 - \frac{2w_i}{C_i}\right) - \alpha_i u_i - \beta_i v_i \right] ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2[\mathrm{g}_i(u_i) + u_i\mathrm{g}_i'(u_i) - v_i\mathrm{p}_i'(u_i) + \theta\alpha_i w_i]ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2[\mathrm{f}_i(v_i) + v_i\mathrm{f}_i'(v_i) - u_i\mathrm{q}_i'(v_i) + \phi\beta_i w_i]ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i[-\mathbf{p}_i(u_i) - \mathbf{q}_i(v_i)]ds + \sum_1^2 \int_{L_{i-1}}^{L_i} n_i r_i \alpha_i[\theta u_i - w_i]ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} m_i r_i \beta_i[\phi v_i - w_i]ds + \sum_1^2 D_{1i}\int_{L_{i-1}}^{L_i} n_i\frac{\partial^2 n_i}{\partial s^2}ds + \sum_1^2 D_{2i}\int_{L_{i-1}}^{L_i} m_i\frac{\partial^2 m_i}{\partial s^2}ds
\end{aligned}$$

Therefore,

$$\begin{aligned}
\dot{V}(t) = \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} [\mathcal{Z}_i r_i^2 + \mathcal{X}_i n_i^2 + \mathcal{Y}_i m_i^2 + 2\mathcal{W}_i r_i n_i + 2\mathcal{U}_i n_i m_i + 2\mathcal{V}_i m_i r_i]ds \\
- \quad & \sum_1^2 D_{1i}\int_{L_{i-1}}^{L_i} \left(\frac{\partial n_i}{\partial s}\right)^2 ds - \sum_1^2 D_{2i}\int_{L_{i-1}}^{L_i} \left(\frac{\partial m_i}{\partial s}\right)^2 ds
\end{aligned}$$

where the functions $\mathcal{X}_i$, $\mathcal{Y}_i$, $\mathcal{Z}_i$, $\mathcal{U}_i$, $\mathcal{V}_i$ and $\mathcal{W}_i$ are given in (7.30). Hence $\dot{V}$ is negative definite if the conditions (7.27) $\to$ (7.29) hold.

We now show that there exist a small subregion of $\mathcal{R} : \{min\{x_1^*, x_2^*\} \leq x_i, u_i \leq max\{x_1^*, x_2^*\},\ min\{y_1^*, y_2^*\} \leq y_i, v_i \leq max\{y_1^*, y_2^*\}\}$, where the system is nonlinearly stable. For this let,

$$\mathcal{N}_{xi} = \frac{x_i \mathrm{g}_i(x_i) - u_i \mathrm{g}_i(u_i)}{x_i - u_i} - y_i \frac{\mathrm{p}_i(x_i) - \mathrm{p}_i(u_i)}{x_i - u_i} + \theta \alpha_i R_i, \tag{7.38}$$

$$\mathcal{N}_{yi} = \frac{y_i \mathrm{f}_i(y_i) - v_i \mathrm{f}_i(v_i)}{y_i - v_i} - x_i \frac{\mathrm{q}_i(y_i) - \mathrm{q}_i(v_i)}{y_i - v_i} + \phi \beta_i R_i, \tag{7.39}$$

$$\mathcal{N}_{zi} = a_i \left(1 - \frac{R_i + w_i}{C_i}\right) - \alpha_i u_i - \beta_i v_i, \tag{7.40}$$

$$\mathcal{N}_{ui} = -\frac{1}{2}[\mathrm{p}_i(u_i) + \mathrm{q}_i(v_i)], \tag{7.41}$$

$$\mathcal{N}_{vi} = \frac{\beta_i}{2}[\phi v_i - R_i], \tag{7.42}$$

$$\mathcal{N}_{wi} = \frac{\alpha_i}{2}[\theta u_i - R_i]. \tag{7.43}$$

then the following nonlinear stability theorem is proved.

Theorem 7.3.3 *The positive continuous steady state solutions of the system is nonlinearly asymptotically stable, for $i = 1, 2$, if,*

$$(i) \quad \mathcal{N}_{xi} \leq 0,\ \mathcal{N}_{yi} \leq 0,\ \mathcal{N}_{zi} \leq 0 \tag{7.44}$$

$$(ii) \quad \mathcal{N}_{ui}^2 \leq 4\mathcal{N}_{xi}\mathcal{N}_{yi} \tag{7.45}$$

$$(iii) \quad \mathcal{N}_{xi}\mathcal{N}_{yi}\mathcal{N}_{zi} + 2\mathcal{N}_{ui}\mathcal{N}_{vi}\mathcal{N}_{wi} \leq \mathcal{N}_{xi}\mathcal{N}_{vi}^2 + \mathcal{N}_{yi}\mathcal{N}_{wi}^2 + \mathcal{N}_{zi}\mathcal{N}_{ui}^2. \tag{7.46}$$

Proof: By using (7.32), (7.33) and (7.31), we get from (7.1), (7.2) and (7.3),

$$\frac{\partial r_i}{\partial t} = r_i \left[a_i \left(1 - \frac{R_i + w_i}{C_i}\right) - \alpha_i u_i - \beta_i v_i\right] - n_i \alpha_i R_i - m_i \beta_i R_i \tag{7.47}$$

$$\frac{\partial n_i}{\partial t} = n_i\left[\frac{x_i\mathbf{g}_i(x_i)-u_i\mathbf{g}_i(u_i)}{x_i-u_i} - y_i\frac{\mathbf{p}_i(x_i)-\mathbf{p}_i(u_i)}{x_i-u_i} + \theta\alpha_i R_i\right] - m_i\mathbf{p}_i(u_i) + r_i\theta\alpha_i u_i + D_{1i}\frac{\partial^2 n_i}{\partial s^2} \tag{7.48}$$

$$\frac{\partial m_i}{\partial t} = m_i\left[\frac{y_i\mathbf{f}_i(y_i)-v_i\mathbf{f}_i(v_i)}{y_i-v_i} - x_i\frac{\mathbf{q}_i(y_i)-\mathbf{q}_i(v_i)}{y_i-v_i} + \phi\beta_i R_i\right] - n_i\mathbf{q}_i(v_i) + r_i\phi\beta_i v_i + D_{2i}\frac{\partial^2 m_i}{\partial s^2} \tag{7.49}$$

Here also, we consider the same positive definite function, as in the case of linear stability,

$$V(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \frac{1}{2}[r_i^2 + n_i^2 + m_i^2]ds$$

From which, we get,

$$\dot{V}(t) = \sum_1^2 \int_{L_{i-1}}^{L_i} \left[r_i\frac{\partial r_i}{\partial t} + n_i\frac{\partial n_i}{\partial t} + m_i\frac{\partial m_i}{\partial t}\right] ds$$

By using (7.47), (7.48) and (7.49), we get,

$$\begin{aligned}
\dot{V}(t) = \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2\left[\frac{x_i\mathbf{g}_i(x_i)-u_i\mathbf{g}_i(u_i)}{x_i-u_i} - y_i\frac{\mathbf{p}_i(x_i)-\mathbf{p}_i(u_i)}{x_i-u_i} + \theta\alpha_i R_i\right] ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2\left[\frac{y_i\mathbf{f}_i(y_i)-v_i\mathbf{f}_i(v_i)}{y_i-v_i} - x_i\frac{\mathbf{q}_i(y_i)-\mathbf{q}_i(v_i)}{y_i-v_i} + \phi\beta_i R_i\right] ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} r_i^2\left[a_i\left(1-\frac{R_i+w_i}{C_i}\right) - \alpha_i u_i - \beta_i v_i\right] ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i[-\mathbf{p}_i(u_i) - \mathbf{q}_i(v_i)]ds + \sum_1^2 \int_{L_{i-1}}^{L_i} m_i r_i\beta_i[\phi v_i - R_i]ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} r_i n_i\alpha_i[\theta u_i - R_i]ds + \sum_1^2 D_{1i}\int_{L_{i-1}}^{L_i} n_i\frac{\partial^2 n_i}{\partial s^2}ds + \sum_1^2 D_{2i}\int_{L_{i-1}}^{L_i} m_i\frac{\partial^2 m_i}{\partial s^2}ds
\end{aligned}$$

Therefore,

$$\begin{aligned}
\dot{V}(t) = \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} [\mathcal{N}_{xi}n_i^2 + \mathcal{N}_{yi}m_i^2 + \mathcal{N}_{zi}r_i^2 + 2\mathcal{N}_{ui}n_i m_i + 2\mathcal{N}_{vi}m_i r_i + 2\mathcal{N}_{wi}r_i n_i]ds \\
- \quad & \sum_1^2 D_{1i}\int_{L_{i-1}}^{L_i}\left(\frac{\partial n_i}{\partial s}\right)^2 ds - \sum_1^2 D_{2i}\int_{L_{i-1}}^{L_i}\left(\frac{\partial m_i}{\partial s}\right)^2 ds
\end{aligned}$$

where the functions $\mathcal{N}_{xi}$, $\mathcal{N}_{yi}$, $\mathcal{N}_{zi}$, $\mathcal{N}_{ui}$, $\mathcal{N}_{vi}$ and $\mathcal{N}_{wi}$ are given by (7.38) → (7.43). Hence $\dot{V}$ is negative definite if the conditions (7.44) → (7.46) hold true, for both $i = 1, 2$.

Now, we consider the uniform steady state case,

7.3.2 The Uniform Steady State: Under Both Sets of Boundary Conditions

Our main purpose of this section is to find the conditions for local and global stability of the uniform steady state, i.e. $R_i(s,t) \equiv C^*$, $x_i(s,t) \equiv K^*$ and $y_i(s,t) \equiv M^*$, for $0 \leq s \leq L_2$, $t \geq 0$, of the system, under both sets of boundary conditions.

Theorem 7.3.4 *The equilibrium (C^*, K^*, M^*) is locally asymptotically stable, for $i = 1, 2$, if the following conditions are satisfied,*

$$(i) \quad H_i^* + \theta\alpha_i C^* \leq 0 \tag{7.50}$$

$$(ii) \quad F_i^* + \phi\beta_i C^* \leq 0 \tag{7.51}$$

$$(iii) \quad [\mathrm{p}_i(K^*) + \mathrm{q}_i(M^*)]^2 \leq 4[H_i^* + \theta\alpha_i C^*][F_i^* + \phi\beta_i C^*], \quad i = 1, 2 \tag{7.52}$$

$$(iv) \quad [H_i^* + \theta\alpha_i C^*][F_i^* + \phi\beta_i C^*]\left[\frac{a_i\phi M^*}{C_i}\right] \leq [F_i^* + \phi\beta_i C^*][\theta K^* - \phi M^*]^2 + \left[\frac{a_i\phi M^*}{C_i}\right][\mathrm{p}_i(K^*) + \mathrm{q}_i(M^*)]^2 \tag{7.53}$$

where

$$H_i^* = \mathrm{g}_i(K^*) + K^*\mathrm{g}_i'(K^*) - M^*\mathrm{p}_i'(K^*) \ \textit{and}\ F_i^* = \mathrm{f}_i(M^*) + M^*\mathrm{f}_i'(M^*) - K^*\mathrm{q}_i'(M^*) \tag{7.54}$$

Proof: Lineariazing the system (7.1)-(7.3), by using

$$R_i(s,t) = C^* + r_i(s,t) \tag{7.55}$$

$$x_i(s,t) = K^* + n_i(s,t) \tag{7.56}$$

$$y_i(s,t) = M^* + m_i(s,t) \tag{7.57}$$

we get,

$$\frac{\partial r_i}{\partial t} = r_i\left[-\frac{a_i C^*}{C_i}\right] - n_i\alpha_i C^* - m_i\beta_i C^* \tag{7.58}$$

$$\frac{\partial n_i}{\partial t} = n_i[\mathrm{g}_i(K^*)+K^*\mathrm{g}_i'(K^*)-M^*\mathrm{p}_i'(K^*)+\theta\alpha_i C^*]-m_i\mathrm{p}_i(K^*)+r_i\theta\alpha_i K^*+D_{1i}\frac{\partial^2 n_i}{\partial s^2} \quad (7.59)$$

$$\frac{\partial m_i}{\partial t} = m_i[\mathrm{f}_i(M^*)+M^*\mathrm{f}_i'(M^*)-K^*\mathrm{q}_i'(M^*)+\phi\beta_i C^*]-n_i\mathrm{q}_i(M^*)+r_i\phi\beta_i M^*+D_{2i}\frac{\partial^2 m_i}{\partial s^2} \quad (7.60)$$

Consider the following positive definite function,

$$\mathrm{V} = \frac{1}{2}\sum_1^2 \int_{L_{i-1}}^{L_i} \left[(x_i - K^*)^2 + (y_i - M^*)^2 + d_i(R_i - C^*)^2\right] \quad (7.61)$$

where d_i, $i = 1, 2$ are positive constants.

Differentiating (7.61) and using (7.58)-(7.60), we get

$$\begin{aligned}
\dot{V} = & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2[H_i^* + \theta\alpha_i C^*]ds + \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2[G_i^* + \phi\beta_i C^*]ds \\
- & \sum_1^2 \int_{L_{i-1}}^{L_i} r_i^2 \left[\frac{d_i a_i C^*}{C_i}\right] ds - \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i[\mathrm{p}_i(K^*) + \mathrm{q}_i(M^*)]ds \\
+ & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i r_i \alpha_i[\theta K^* - d_i C^*]ds + \sum_1^2 \int_{L_{i-1}}^{L_i} m_i r_i \beta_i[\phi M^* - d_i C^*]ds \\
+ & \sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} n_i \frac{\partial^2 n_i}{\partial s^2} ds + \sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} m_i \frac{\partial^2 m_i}{\partial s^2} ds \qquad (7.62)
\end{aligned}$$

Integrating by parts and using the matching conditions at the interface and for both set of boundary conditions, we get

$$\sum_1^2 \int_{L_{i-1}}^{L_i} D_{1i} n_i \frac{\partial^2 n_i}{\partial s^2} ds = -\sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial n_i}{\partial s}\right)^2 ds \quad (7.63)$$

$$\sum_1^2 \int_{L_{i-1}}^{L_i} D_{2i} m_i \frac{\partial^2 m_i}{\partial s^2} ds = -\sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial m_i}{\partial s}\right)^2 ds. \quad (7.64)$$

Choosing d_i, for $i = 1, 2$, such that, the coefficients of $m_i r_i$ become zero, i.e. $d_1 = d_2 = \phi M^*/C^*$. Therefore, from (7.62), $\dot{V}$ is negative definite, if the conditions (7.50), (7.51), (7.52) and (7.53) are satisfied. ∎

Moreover,

Theorem 7.3.5 *Let $H_i^* + \theta\alpha_i C^* > 0$ and/or $F_i^* + \phi\beta_i C^* > 0$. Then the equilibrium*

(C^*,K^*,M^*) is locally asymptotically stable, if the conditions (7.52) and (7.53) along with

$$H_i^* + \theta\alpha_i C^* \le D_{1i}\frac{\pi^2}{(L_i - L_{i-1})^2}, \text{ and } F_i^* + \phi\beta_i C^* \le D_{2i}\frac{\pi^2}{(L_i - L_{i-1})^2} \tag{7.65}$$

for $i = 1, 2$, hold.

Proof: By using Poincare's Inequality, we get

$$D_{1i}\int_{L_{i-1}}^{L_i}\left[\frac{\partial n_i}{\partial s}\right]^2 ds \le D_{1i}\frac{\pi^2}{(L_i - L_{i-1})^2}\int_{L_{i-1}}^{L_i} n_i^2 ds$$

and

$$D_{2i}\int_{L_{i-1}}^{L_i}\left[\frac{\partial m_i}{\partial s}\right]^2 ds \le D_{2i}\frac{\pi^2}{(L_i - L_{i-1})^2}\int_{L_{i-1}}^{L_i} m_i^2 ds$$

Therefore from (7.62), using (7.63) and (7.64) and choosing $d_i = \phi M^*/C^*$, for $i = 1, 2$, we get,

$$\begin{aligned}
\dot{V} = \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i^2[H_i^* + \theta\alpha_i C^* - D_{1i}\frac{\pi^2}{(L_i - L_{i-1})^2}]ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} m_i^2[G_i^* + \phi\beta_i C^* - D_{2i}\frac{\pi^2}{(L_i - L_{i-1})^2}]ds \\
- \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} r_i^2\left[\frac{a_i\phi M^*}{C_i}\right]ds - \sum_1^2 \int_{L_{i-1}}^{L_i} n_i m_i[\mathbf{p}_i(K^*) + \mathbf{q}_i(M^*)]ds \\
+ \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} n_i r_i \alpha_i[\theta K^* - \phi M^*]ds
\end{aligned}$$

Hence the theorem. ∎

We now state the global stability of the uniform steady state,

Theorem 7.3.6 *The uniform steady-state (C^*,K^*,M^*) is globally asymptotically stable if*

$$A_i = \frac{x_i\mathbf{g}_i(x_i) - M^*\mathbf{p}_i(x_i)}{x_i - K^*} + \theta\alpha_i C^* \le 0, \tag{7.66}$$

$$\mathcal{B}_i = \frac{y_i \mathbf{f}_i(y_i) - K^* \mathbf{q}_i(y_i)}{y_i - M^*} + \phi\beta_i C^* \leq 0, \tag{7.67}$$

$$\left[\frac{\mathbf{p}_i(x_i)}{x_i} + \frac{\mathbf{q}_i(y_i)}{y_i}\right]^2 \leq 4\frac{\mathcal{A}_i\mathcal{B}_i}{x_i y_i}, \tag{7.68}$$

and

$$\frac{\mathcal{A}_i\mathcal{B}_i a_i}{x_i y_i C_i} \leq \beta_i^2 \mathcal{A}_i[\phi - 1]^2 + \alpha_i^2 \mathcal{B}_i[\theta - 1]^2 + \frac{a_i}{C_i}\left[\frac{\mathbf{p}_i(x_i)}{x_i} + \frac{\mathbf{q}_i(y_i)}{y_i}\right]^2. \tag{7.69}$$

Proof: Let us consider the following positive definite function,

$$\begin{aligned} V(x, y, R) = \quad & \sum_1^2 \int_{L_{i-1}}^{L_i} \left(x_i - K^* - K^* ln\frac{x_i}{K^*}\right) ds + \sum_1^2 \int_{L_{i-1}}^{L_i} \left(y_i - M^* - M^* ln\frac{y_i}{M^*}\right) ds \\ + & \sum_1^2 \int_{L_{i-1}}^{L_i} \left(R_i - C^* - C^* ln\frac{R_i}{C^*}\right) \end{aligned} \tag{7.70}$$

Differentiating (7.70) with respect to t, and using (7.1) and (7.2), we get,

$$\begin{aligned} \dot{V}(s,t) &= \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} \left[\left(\frac{x_i - K^*}{x_i}\right)\frac{\partial x_i}{\partial t} + \left(\frac{y_i - M^*}{y_i}\right)\frac{\partial y_i}{\partial t} + \left(\frac{R_i - C^*}{R_i}\right)\frac{\partial R_i}{\partial t}\right] ds \\ &= \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} \frac{(x_i - K^*)^2}{x_i}\left[\frac{x_i \mathbf{g}_i(x_i) - M^* \mathbf{p}_i(x_i)}{x_i - K^*} + \theta\alpha_i C^*\right] ds \\ &+ \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} \frac{(y_i - M^*)^2}{y_i}\left[\frac{y_i \mathbf{f}_i(y_i) - K^* \mathbf{q}_i(y_i)}{y_i - M^*} + \phi\beta_i C^*\right] ds \\ &- \sum_1^2 \int_{L_{i-1}}^{L_i} (R_i - C^*)^2 \left[\frac{a_i}{C_i}\right] ds - \sum_1^2 \int_{L_{i-1}}^{L_i} (x_i - K^*)(y_i - M^*)\left[\frac{\mathbf{p}_i(x_i)}{x_i} + \frac{\mathbf{q}_i(y_i)}{y_i}\right] ds \\ &+ \sum_1^2 \int_{L_{i-1}}^{L_i} (y_i - M^*)(R_i - C^*)\left[\beta_i(\phi - 1)\right] ds \\ &+ \sum_1^2 \int_{L_{i-1}}^{L_i} (R_i - C^*)(x_i - K^*)\left[\alpha_i(\theta - 1)\right] ds \\ &+ \sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} \frac{x_i - K^*}{x_i}\frac{\partial^2 x_i}{\partial s^2} ds + \sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} \frac{y_i - M^*}{y_i}\frac{\partial^2 y_i}{\partial s^2} ds \end{aligned}$$

Now since, under both set of boundary conditions,

$$[x_1(0,t) - K^*]\frac{\partial x_1}{\partial s}(0,t) = [x_2(L_2,t) - K^*]\frac{\partial x_2}{\partial s}(L_2,t) = 0 \tag{7.71}$$

$$[y_1(0,t) - M^*]\frac{\partial y_1}{\partial s}(0,t) = [y_2(L_2,t) - M^*]\frac{\partial y_2}{\partial s}(L_2,t) = 0 \tag{7.72}$$

Then the integrals,

$$I_1 = \sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} \frac{x_i - K^*}{x_i} \frac{\partial^2 x_i}{\partial s^2} ds = -\sum_1^2 D_{1i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial x_i}{\partial s}\right)^2 ds \tag{7.73}$$

and

$$I_2 = \sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} \frac{y_i - M^*}{y_i} \frac{\partial^2 y_i}{\partial s^2} ds = -\sum_1^2 D_{2i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial y_i}{\partial s}\right)^2 ds \tag{7.74}$$

Hence $\dot{V}(K^*, M^*, C^*) = 0$ and $\dot{V}(x,y) < 0$, if the conditions (7.66) $\rightarrow$ (7.69) are satisfied. Therefore $\dot{V}(x,y)$ is negative definite over $x > 0$, $y > 0$, $R > 0$ with respect to $x_i^* = K^*$, $y_i^* = M^*$, $R_i^* = C^*$, proving the theorem. ∎

Remark: On comparing the analysis of this chapter with chapter-6, we may conclude that the role of supplementary resource is to increase the level of nonuniform steady state at each point of the habitat. As before, the role of patchiness is destabilizing in presence of supplementary resource also, which we can note by comparing the cases of non-uniform and uniform steady states in a patchy habitat.

7.4 Numerical Example

We discuss here a numerical example, to study the behavior of the steady state solutions of the above system and compare it with the case of a competing species without supplementary resource in a two-patch habitat, as described in chapter-6. For this we consider the following particular form of functions:

$$\mathrm{g}_i(u_i) = r_i\left(1 - \frac{u_i}{K_i}\right),\ \mathrm{f}_i(v_i) = s_i\left(1 - \frac{v_i}{M_i}\right),\ \mathrm{p}_i(u_i) = e_i u_i,\ \mathrm{q}_i(v_i) = b_i v_i,\quad i = 1,2$$

also for simplicity take, $C_1 = C_2 = C$. Then the steady state of the above system takes the

$$u_i\left[r_i\left(1 - \frac{u_i}{K_i}\right) + \frac{\theta\alpha_i C}{a_i}(a_i - \alpha_i u_i)\right] - v_i\left[e_i u_i + \frac{\theta\alpha_i\beta_i C}{a_i}u_i\right] = 0 \tag{7.75}$$

$$D_{2i}\frac{d^2v_i}{ds^2} + v_i\left[s_i\left(1-\frac{v_i}{M_i}\right) + \frac{\phi\beta_i C}{a_i}(a_i - \beta_i v_i)\right] - u_i\left[b_i v_i + \frac{\phi\alpha_i\beta_i C}{a_i}v_i\right] = 0 \tag{7.76}$$

with reservoir boundary conditions

$$u_1(0) = x_1^{**}, u_2(L_2) = x_2^{**}, \quad \text{and } v_1(0) = y_1^{**}, v_2(L_2) = y_2^{**}, \tag{7.77}$$

and the continuity and flux matching conditions at the interface $s = L_1$,

$$D_{11}\frac{du_1}{ds}(L_1) = D_{12}\frac{du_2}{ds}(L_1),\ D_{21}\frac{dv_1}{ds}(L_1) = D_{22}\frac{dv_2}{ds}(L_1), \text{ and} \tag{7.78}$$

$$u_1(L_1) = u_2(L_1), v_1(L_1) = v_2(L_1). \tag{7.79}$$

We solve the system (7.75)-(7.79) numerically, for the following set of parameters, $L_1 = 10$, $L_1 = 20$, $D_{11} = 0.8$, $D_{12} = 0.8$, $D_{21} = 0.8$, $D_{22} = 0.8$, $r_1 = 0.115$, $r_2 = 0.825$, $a_1 = 1.0$, $a_2 = 1.0$, $s_1 = 0.135$, $s_2 = 0.3$, $e_1 = 5.0E{-}05$, $e_2 = 5.0E{-}05$, $b_1 = 4.0E{-}05$, $b_2 = 6.0E-05$, $K_1 = 57.5$, $K_2 = 165$, $M_1 = 33.75$, $M_2 = 150$, $\alpha_1 = 5.0E-05$, $\alpha_2 = 2.0E-05$, $C = 60$, $\beta_1 = 5.0E-04$, $\gamma_2 = 7.0E-04$, $\theta = 0.4$, and $\phi = 0.8$, and the plot of the steady state solutions are shown in Fig.6.1. By using the above values of the parameters, we get, $x_1^{**} = 63.20 > x_1^* = 55.88$, $x_2^{**} = 176.38 > x_2^* = 162.16$, $y_1^{**} = 35.92 > y_1^* = 32.35$, and $y_2^{**} = 181.18 > y_2^* = 141.90$. As in chapter-5, it is noted from the figure that, in presence of a renewable supplementary resource, also the steady state solutions are continuous, monotonic and the level of both the species are higher at each point of the habitat.

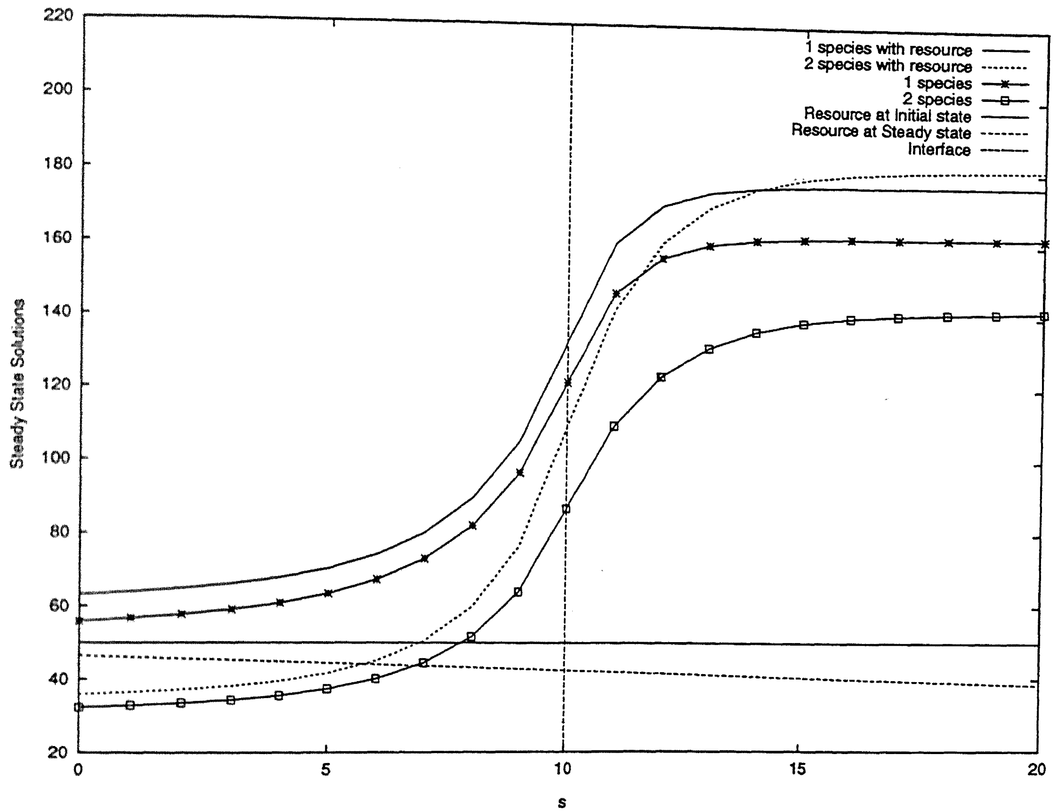


Figure 7.1: The steady state solutions for both the species, with and without a common supplementary resource for both the species

7.5 Summary

In chapter-6, we have discussed the existence and stability of the non-uniform steady state corresponding to two competing species system in a two patch habitat with diffusion. In this chapter, the same ecological problem is modelled and analyzed when there is a non-diffusing renewable common resource for each of the competing population in both the patches. It has been assumed that both the competing population follow a general type of logistic growth in each of the patches, as in the previous chapter. Also, the self-renewable supplementary resource is logistically growing but non-diffusing.

It has been shown, as in chapter-6, that there exists a positive, monotonic, continuous steady state solution with continuous matching conditions at the interface for both the species separately. The conditions for asymptotic stability in both linear and nonlinear cases under both set of boundary conditions have also been obtained. It has been further shown that in presence of supplementary resource the level of steady state distribution is correspondingly greater and the effect of patchiness is destabilizing even in presence of a common self-renewable supplementary resource.

Bibliography

1. **Butler, G.J.** and **Wolkowicz**, *A mathematical model of the chemostat with a general class of functions describing nutrient uptake*, SIAM J. Appl. Math., **45**(1), (198x5).

2. **Freedman, H.I.** and **Kriszti, T.**, *Global stability in model of population dynamics with diffusion. I. Patchy Environment*, Proc. Royal Soci. of Edinburgh, **122A**, 69-84 (1992).

3. **Freedman, H.I.**, **Shukla, J.B.** and **Takeuchi, Y.**, *Population diffusion in a two-patch environment*, Mathl. Biosci., **95**, 111-123 (1989).

4. **Freedman, H.I.** and **Shukla, J.B.**: *The effect of a predator resource on a diffusive predator-prey system*, Natural Resources Modelling, **3**(3), (1989).

5. **Freedman, H.I.** and **So, J.W.H.**, *Global stability and persistence of simple food chains*, Mathl. Biosci., **76**, 69-86 (1985).

6. **Freedman, H.I.** and **Wu, J.**, *Steady state analysis in a model for population diffusion in a multi-patch environment*, Nonl. Analy., Theor., Meths. & Appl., **18**(6), 517-542 (1992).

7. **Gopalsamy, K.**, *Convergence in a resource-based competition system*, Bull. Math. Biol., **48**(5/6), 681-699, (1986).

8. **Hadeler, K.P.**, **Heiden, V.** and **Rothe, F.**, *Nonhomogeneous spatial distributions of populations*, J. Math. Biol., **1**, 165-176 (1974).

9. **Herbert, D.**, **Elsworth** and **Telling, R.C.**, *The continuous culture of bacteria: a theoretical and experimental study*, J. Gen. Microbiol., **4**, 601-622, (1956).

10. **Hsu, S.B.**, *On a resource based ecological competition model with interference*, J. Math. Biol., **12**, 45-52, (1981).

11. **Hsu, S.B.**, *Limiting behavior for competing species*, SIAM J. Appl. Math., **34**(4), (1978).

12. **Hsu, S.B., Cheng, K.S.** and **Hubbell, S.P.**, *Exploitative competition of Microorganisms for two complementary nutrients in continuous cultures*, SIAM J. Appl. Math., **41**, 422-444, (1981).

13. **Hsu, S.B., Hubbell, S.P.** and **Waltman, P.**, *A mathematical theory of single-nutrient competitions in continuous cultures of microorganism*, SIAM J. Appl. Math., **32**, 366-383 (1977).

14. **Leon, J.A.** and **Tumpson, D.B.**, *Competition between two species for two complementary or two substituble resources*, J. Theor. Biol., **50**, 185-201, (1975).

15. **Levin, S.A.**, *Population model and community structure in heterogeneous environments, in Mathematical Ecology*, Hallam, T.G. and Levin, S.A., eds., Springer, New York, 295-321 (1986).

16. **Mitra, D, Mukherjee, D.** and **Roy, A.B.**, *Permanent coexistence in a resource-based competition system*, Ecol. Modelling, **60**, 77-85 (1992).

17. **Novick, A.** and **Szilard, L.**, *Description of the chemostat*, Science, **112**, 715-716, (1950).

18. **Okubo, A.**, *Diffusion and Ecological Problem: Mathematical models*, Lecture Notes, Springer-Verlag (1980).

19. **Rothe, F.**, *Global Solution of Reaction-Diffusion Systems*, Lecture Notes in Mathematics, **1072**, Springer-Verlag (1984).

20. **Shukla, J.B.** and **Verma, S.**, *Effects of convective and dispersive interactions on the stability of two species*, Bul. Math. Biol., **43**, 593-610 (1981).

21. **Shukla, V.P., Shukla, J.B.** and **Das, P.C.**, *Environmental effects on the linear stability of a three species food chain model*, Mathl. Biosci., **57**, 35-58 (1981).

22. **Williams, F.M.**, *Dynamics of microbial populations*, Systems Analysis and Simulation in Ecology, B.Patten, ed., Academic Press, New York, Chapter 3, (1971).

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